

Chapter 3

Artificial Production

Key Questions:

- What are the potential benefits of artificial production programs?*
- What are the types of hatchery programs currently operated for steelhead in Washington and what has been the survival rate for the juveniles released?*
- What is the fitness (or adult-to-adult survival) of naturally-spawning steelhead of hatchery-origin relative to the indigenous population?*
- What are the potential genetic and ecological effects of artificial production on natural populations? How do hatchery facilities, hatchery effluent, or the release of diseased fish affect natural populations?*

3.1 Introduction

Over 9.1 million juvenile steelhead were released from artificial production programs in Washington in 2000, a nearly four-fold increase from 1960 (Fig. 3-1). In this chapter we evaluate the economic and conservation benefits of hatchery programs as well as the potential risks they may pose to natural populations.

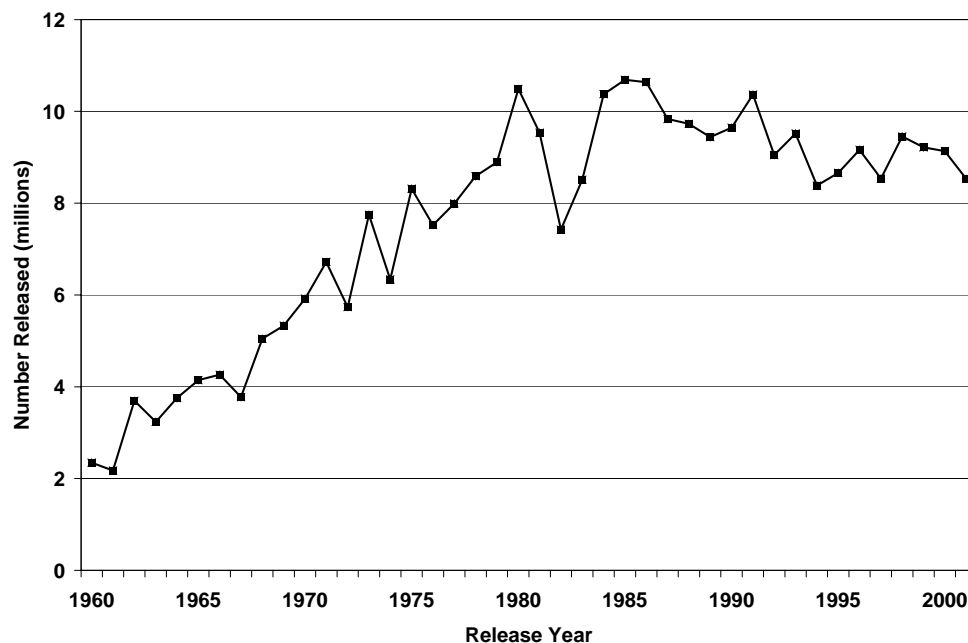


Figure 3-1. Tribal, federal, and state releases of summer and winter steelhead smolts in Washington.

3.2 Artificial Production Programs

3.2.1 Programs Types and Benefits

The primary objectives of hatchery programs are to enhance harvest opportunities or to provide recovery, or conservation benefits. Hatchery-origin steelhead provide substantial recreational and economic benefits to Washington State residents and comprise the vast majority of the recreational fishery harvest of steelhead (96% of recreational fishery harvest in 2003-2004). In the nine seasons from 1995-1996 through 2003-2004, recreational anglers harvested an average of 99,300 hatchery-origin

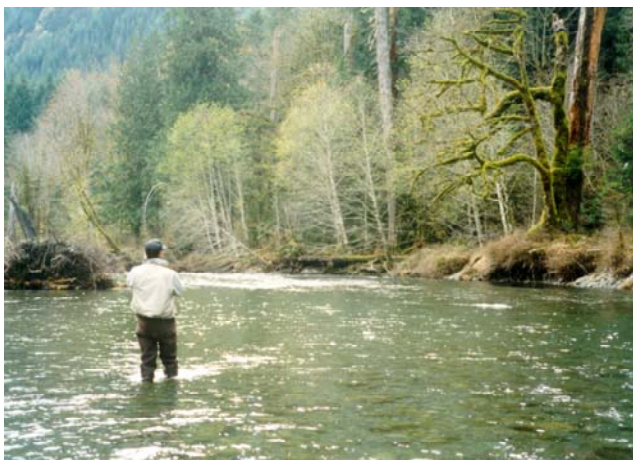


Photo 3-1. The total economic impact of the catch of hatchery-origin steelhead in recreational fisheries is estimated at over \$188 million annually. Photo source: unknown.

steelhead. With an estimated expenditure of \$999 per fish caught, (see Box 3-1, Economic Analysis), the average total expenditures associated with hatchery-origin steelhead was approximately \$99 million. The total economic impact of this catch is estimated at over \$188 million. The average annual production of steelhead from hatcheries in Washington during this time period was 8.8 million fish. With an estimated production cost of about \$0.50 per fish, the cost of steelhead released exceeds \$4.4 million per year but provides a benefit:cost ratio of more than 40:1 for recreational fisheries alone.

Hatchery programs can also have significant conservation benefits. According to the NMFS "Policy on the Consideration of Hatchery-Origin Fish in Endangered Species Act Listing Determination for Pacific Salmon and Steelhead" (70 FR 37204), hatchery-origin fish can positively affect the status of an ESU by:

- 1) "contributing to increasing abundance and productivity of the natural populations in the ESU";
- 2) "improving spatial distribution";
- 3) "serving as a source population for repopulating unoccupied habitat"; and
- 4) "conserving genetic resources of depressed natural populations in the ESU".

Hatchery programs, although quite diverse in details, can be simply classified by management objective and reproductive strategy used to achieve the objective

Box 3-1. Economic Analysis of Recreational Harvest of Steelhead

The economic analysis of the recreational harvest of steelhead is derived from a survey conducted by the U.S. Census Bureau in 2001. Detailed information on sampling procedures, response rates, and survey results can be found in U.S. Department of the Interior et al. (2003) and Southwick and Associates (2003).

We assessed the annual expenditures and economic benefit of the recreational harvest of steelhead in Washington using the following five steps: 1) estimate the average expenditures per day of steelhead fishing in the western states; 2) estimate the total expenditures of steelhead fishers in Washington; 3) estimate the expenditures per steelhead caught by recreational fishers; 4) estimate the economic output per steelhead caught by recreational fishers; and 5) estimate the average expenditures and economic output associated with the catch of hatchery-origin steelhead.

Step 1. Average Expenditures Per Day of Steelhead Fishing

The average expenditure per day of steelhead fishing was estimated from data in Southwick and Associates for steelhead fishers in the western states.

Expenditures	\$327,088,084	Southwick and Associates, page 186
Days Fished for Steelhead	4,911,643	Southwick and Associates, page 89
Expenditures per Day	\$67	

Step 2. Total Expenditures by Steelhead Fishers in Washington

We estimated the total expenditures by steelhead fishers in Washington by multiplying the total estimated days of steelhead fishing by the average expenditures per day computed in Step 1. This assumes that steelhead fishers in Washington expend the same amount of money per day of fishing as the average steelhead fisher in the western states.

Expenditures per Day	\$67	Step 1
Days Fished for Steelhead	2,483,000	U.S. Department of Interior et al. (2003), Table 7
Total Expenditures	\$166,361,000	

Step 3. Expenditures per Steelhead Caught by Steelhead Fishers

We estimated the expenditures per steelhead caught by dividing the total expenditures computed in Step 2 by the total catch of steelhead in the 2001 calendar year.

Total Expenditures	166,361,000	Step 2
2001 Calendar Year Catch	166,453	WDFW catch estimates
Expenditures per Steelhead Caught	\$999	

Box 3-1 (continued).

Step 4. Economic Output per Steelhead Caught

We estimated the economic output per steelhead caught by multiplying the expenditures per steelhead caught by an economic output multiplier. The economic multiplier estimates the ripple effect of how each dollar spent by a fisher "increase another person's income, enabling the person (or business) to spend more, which in turn increases income for someone else" (ASA 2002). We assumed that the economic multiplier computed for the aggregate of all types of sport fishing in Washington was applicable to steelhead fishers.

Expenditures per Steelhead Caught	\$999	Step 3
Economic Multiplier	1.9	ASA (2002)
Economic Benefit per Steelhead Caught	\$1,898	

Step 5. Average Expenditures and Economic Output

We estimated the average expenditures and economic output associated with the catch of steelhead of hatchery origin by multiplying the average catch in the 1995-1996 through 2003-2004 seasons by the expenditures (Step 3) and economic output (Step 4) per steelhead caught. All economic analyses are in 2001 dollars.

Region	Average catch hatchery-origin steelhead	Recreational fisher expenditures	Economic output
Puget Sound & Strait of Juan de Fuca	13,981	\$14.0 million	\$26.5 million
Washington Coast	12,625	\$12.6 million	\$24.0 million
Columbia Basin	72,657	\$72.6 million	\$137.9 million
Total	99,263	\$99.2 million	\$188.4 million

The estimated expenditures by recreational fishers associated with the catch of hatchery-origin steelhead is approximately \$99 million, with an estimated economic output of \$188 million.

(Table 3-1). The two primary management objectives for hatchery programs are recovery/conservation or harvest. Programs with a harvest objective are often mitigation for production lost through the construction of dams or other anthropogenic factors. For example, the Lower Snake River Compensation Plan is a congressionally authorized mitigation program that is intended to compensate for natural production lost as a result of the construction of dams in the Snake River basin. The two reproductive strategies used to achieve the objective, integrated or isolated, differ in the degree of reproductive interaction between natural and hatchery-origin adults in the hatchery and natural spawning areas. Integrated programs intend fish of natural- and hatchery-origin to be reproductively connected to represent a single population. This requires natural-origin adults in the hatchery broodstock, and hatchery-origin adults in the natural spawning areas. Isolated programs (called segregated in HSRG 2004) intend for the hatchery population to be a distinct and reproductively isolated from naturally-spawning populations. Strategy selection is program- and watershed-specific, and depends on the status of the natural population, the quality of the habitat, the ability to collect natural-origin broodstock, the ability to control the number of hatchery-origin adults in natural spawning areas, and the objectives of the program.

Table 3-1 Artificial production strategies and their primary uses (from PSTT and WDFW 2004).

Primary Management Objective	Reproductive Strategy	
	Integrated Production	Isolated Production
Recovery	<ul style="list-style-type: none"> • Prevent extinction • Increase natural origin recruits using the local stock • Reintroduction • Research 	<ul style="list-style-type: none"> • Prevent extinction • Create 'reserve' population in case other recovery options fail • Gene banking until reintroduction • Research
Harvest	<ul style="list-style-type: none"> • When isolated approach is not feasible • Maintaining local stocks • During rebuilding • Mitigation • Research 	<ul style="list-style-type: none"> • Create new or enhance existing fishing opportunities • Mitigation • Allocation • Research

Many of the steelhead programs with a recovery objective are located in the Snake River and Upper Columbia basins. In the Upper Columbia River region, steelhead programs operated from Eastbank and Wells hatcheries produce summer steelhead with

release sites that include the Wenatchee River and its tributaries, the Methow River and its tributaries, and the Okanogan River and its tributaries. In the biological opinion for this program, the NMFS (2002) concluded that: "Overall, the artificial propagation programs provide a benefit to the endangered UCR steelhead ESU by boosting the population abundance, while maintaining or increasing the genetic diversity, and spatial distribution."

At broodstock collection sites in Washington, there are 33 facilities that gather brood stock for isolated harvest programs, 4 sites for integrated harvest, 1 site for integrated recovery, 8 sites for integrated harvest and recovery, 2 sites for integrated harvest and research, and 2 sites for integrated recovery and research (Table 3-2).

Isolated artificial production programs for steelhead in western Washington rely almost exclusively on broodstock that originated from one of two sources - Chambers Creek winter steelhead or Skamania summer steelhead. The Chambers Creek winter steelhead (South Puget Sound) program was initiated in 1945 at the South Tacoma Hatchery and the Skamania summer steelhead (lower Columbia River) program in 1956 (Crawford 1979). Both stocks were developed to produce smolts in a one-year rearing program compared to the typical two year freshwater residence of steelhead rearing in the natural habitat of Washington (Pautzke and Meigs 1940; Larson and Ward 1954; Crawford 1979). The Chambers Creek stock was selected for early spawn timing; maturity in adults was further accelerated in the warm (55-58° F) water at Chambers Creek Hatchery and nearby South Tacoma Hatchery. Consequently, adult return timing advanced from March-May to December-January, with most spawning completed by the end of January. The Skamania Hatchery summer steelhead stock was started with broodstock from the Washougal and Klickitat rivers. Skamania steelhead were also selected for early spawn timing and adult fish now typically spawn in December-January compared to February-April for wild fish (Crawford 1979).

Programs that use an isolated reproductive strategy can use eggs (or juveniles) that originate from either adults returning to the facility, other facilities within the watershed, or facilities outside of the watershed. Historically, the latter approach was often used in western Washington because of the operational simplicity, flexibility, and cost. Eggs were imported from a few centrally located facilities (e.g., South Tacoma Hatchery) with adequate water temperatures to assure development was accelerated to meet a one-year release schedule. Alternatively, if broodstock are collected onsite, additional costs may be incurred for spawning and incubation, and fishery management may have to be adjusted to ensure sufficient adults return to the facility to meet broodstock requirements. To reduce out of watershed transfers and accelerate early growth and development to achieve optimum release size of juvenile steelhead within 12 to 16 months, heated water systems (\$5,000 capital, \$2,500 annual operating costs) have been installed at some hatcheries.

Table 3-2. Steelhead broodstock collection sites, broodstock origin, run timing, program strategy, and program objective. (Run timing is defined as W for Winter or S for Summer).

Geographic Location	Facility	Broodstock Origin	Run Timing	Strategy	Objective
Puget Sound Hood Canal	Kendall Creek	Chambers	W	Isolated	Harvest
	Marblemount	Chambers	W	Isolated	Harvest
	Barnaby Slough	Chambers	W	Isolated	Harvest
	Whitehorse Ponds	Chambers	W	Isolated	Harvest
	Reiter Ponds	Skamania	S	Isolated	Harvest
	Tokul Creek	Chambers	W	Isolated	Harvest
	Palmer Ponds	Chambers	W	Isolated	Harvest
	Palmer Ponds	Skamania	S	Isolated	Harvest
	Soos	Chambers	W	Isolated	Harvest
	Soos ¹	Local	W	Integrated	Recovery
	Puyallup	Chambers	W	Isolated	Harvest
	Hamma Hamma ²	Local	W	Integrated	Recovery & Research
Strait of Juan de Fuca	Dungeness	Chambers	W	Isolated	Harvest
	Lower Elwha ³	Chambers	W	Isolated	Harvest
	Hoko ⁴	Chambers	W	Isolated	Harvest
Olympic Peninsula	Makah NFH ⁵	Quinalt	W	Isolated	Harvest
	Snider Creek	Local	W	Integrated	Harvest
	Bogachiel	Chambers	W	Isolated	Harvest
	Bogachiel	Skamania	S	Isolated	Harvest
	Quinalt NFH ⁵	Unknown	W	Isolated	Harvest
	Lake Quinalt ⁶	Local	W	Integrated	Harvest
Grays Harbor	Humptulips	Chambers	W	Isolated	Harvest
	Lake Aberdeen	Chambers	W	Isolated	Harvest
	Lake Aberdeen	Local	W	Integrated	Harvest
	Lake Aberdeen	Skamania	S	Isolated	Harvest
	Bingham	Local	W	Integrated	Harvest & Recovery
	Skookumchuck	Local	W	Integrated	Harvest
	Eight ⁷	Local	W	Integrated	Harvest & Recovery

¹ Program operated by Muckleshoot Tribe.

² Cooperative program with Long Live the Kings and NOAA.

³ Program operated by Lower Elwha Klallam Tribe.

⁴ Program operated by the Makah Tribe.

⁵ Program operated by the Fish and Wildlife Service.

⁶ Program operated by the Quinalt Indian Nation.

⁷ Cooperative program with the Upper Chehalis Fisheries Enhancement Group.

Table 3-2 (continued). Steelhead broodstock collection sites, broodstock origin, race, program strategy, and program objective. (Run timing is defined as W for Winter or S for Summer).

Geographic Location	Facility	Broodstock Origin	Run Timing	Strategy	Objective
Willapa Bay	Forks Creek	Chambers	W	Isolated	Harvest
	Naselle	Chambers	W	Isolated	Harvest
Lower Columbia	Elochoman	Chambers	W	Isolated	Harvest
	Cowlitz Trout	Local	W	Integrated	Harvest & Recovery
	Cowlitz Trout	Chambers	W	Isolated	Harvest
	Cowlitz Trout	Skamania	S	Isolated	Harvest
	Kalama Falls	Chambers	W	Isolated	Harvest
	Kalama Falls	Local	W	Integrated	Harvest & Research
	Kalama Falls	Skamania	S	Isolated	Harvest
	Kalama Falls	Local	S	Integrated	Harvest & Research
	Merwin	Chambers	W	Isolated	Harvest
	Merwin	Skamania	S	Isolated	Harvest
	Skamania	Chambers	W	Isolated	Harvest
	Skamania	Skamania	S	Isolated	Harvest
Middle Columbia	Cle Elum	Local	S	Integrated	Recovery & Research
	Lyons Ferry	Local (Touchet)	S	Integrated	Harvest & Recovery
Upper Columbia	Eastbank	Wenatchee	S	Integrated	Harvest & Recovery
	Wells	Local (Methow/Okanogan)	S	Integrated	Harvest & Recovery
	Cassimer Bar ¹	Local (Okanogan)	S	Integrated	Harvest & Recovery
Snake River	Cottonwood	Wallowa	S	Isolated	Harvest
	Lyons Ferry	Wallowa Wells	S	Isolated	Harvest
	Lyons Ferry	Local (Touchet)	S	Integrated	Harvest Recovery

¹ Program operated by the Confederated Tribes of the Colville Reservation.

An integrated program requires collection and spawning of natural-origin steelhead brood stock throughout the protracted return and spawn. In addition, heated incubation water and higher protein diets may be necessary for progeny to achieve the optimal release size for survival. Replacing a 150,000 juvenile steelhead isolated program with an integrated late brood stock program may cost about \$5,000 in initial capital, and \$12,000 in annual operating costs (\$4,000 energy, \$8,000 in feed costs). Additional costs would be incurred to collect natural-origin broodstock based upon specific hatchery needs to include traps, holding structures, transport trucks for broodstock collected through angling efforts during the protracted adult return, etc.

A relatively new method for increasing the abundance of natural-origin adult steelhead, which takes advantage of their iteroparity nature, has been the reconditioning of spawned out adults (kelts). This is especially important on the Columbia River, where repeat spawning is complicated by survival through the dams (Wertheimer and Evans 2005). However, the dams also afford the opportunity to collect steelhead kelts for reconditioning (Evans and Beaty 2001). On the Yakima River, kelts are captured at the Chandler Canal and directed into the adjacent Yakama Nation hatchery in Prosser. The kelts are treated for parasites and pathogens and restarted on feed to regain body condition. Some fish are reconditioned for a short time (one to three months) and then transported for release downstream of Bonneville Dam to return to the ocean. Others are held and released the following winter in the Yakima River to spawn. In 2004, survival of kelts from capture to release for short-term reconditioning was 79%, while long-term reconditioning was 40% (Hatch et al. 2004; Branstetter et al. 2005). Reconditioned fish radio-tagged and released in the Yakima River have subsequently been detected in spawning tributaries (Branstetter et al. 2005). Reconditioning efforts require cool well water, adult holding areas, labor and special diet, but the increase to natural production could be relatively high through a minimally invasive manner.

3.2.2 Survival Rates of Hatchery Fish

Factors Affecting Survival Rates

One important performance measure for programs with either a harvest or recovery objective is the survival rate, or the number of adult fish that return per juvenile released. Research indicates that hatchery steelhead have the highest survival rate when released at 75-90 grams (Larson and Ward 1955; Royal 1973; Wagner et al. 1963; Buchanan 1977; Tipping et al. 1995; Tipping 1997) with a condition factor of 0.90-0.99 (Tipping et al. 1995; Tipping and Byrne 1996) starting in mid-April through mid-May (Wagner 1968; Royal 1973; Gearheard 1981). In addition, rearing fish in semi-natural rearing ponds enhances post-release survival (Tipping 1998a; 2001a), forced releases outperform volitional releases (Wagner 1968; Evenson and Ewing 1992) and seasonally cool water temperatures appear to increase post-release survival (Bjorn 1984). Juvenile

steelhead are generally indifferent to rearing factors such as density and loading (Tipping et al. 2004), stress from trucking (Columbia River Transportation Ad Hoc Review Group 1992; Tipping 1998b), hand- versus demand- feeding (Tipping 2001b), exercise (Evenson and Ewing 1993), and acclimation (Kenaston et al. 2001) in the range of conditions typically encountered in WDFW facilities. Precocity, an undesired by-product of hatchery rearing (McMichael et al. 1997), increases with growth rates and may be hatchery specific (Tipping et al. 2003).

NATURES and Semi-Natural Rearing

Natural rearing systems (NATURES) rearing involves adding materials or altering culture methods so juvenile salmonids are exposed to a more natural environment that also increases their adult survival. Since wild fish commonly have greater adult survival than hatchery fish, naturalizing the hatchery environment has potential to increase adult survival of hatchery fish. Obviously, if NATURES rearing increased adult survivals, great economic benefit would result at relatively little expense. Earthen/gravel rearing ponds are commonly used semi-natural hatchery vessels that generally produce better quality smolts than fish reared in concrete raceways (Piper et al. 1992).

Maynard et al. (1995) reviewed semi-natural culture strategies for enhancing survivals of anadromous salmonids. These included rearing fish over natural substrates for proper cryptic coloration, training fish to avoid predators, exercise to enhance the fish's ability to escape predation, supplementing with live food to improve foraging ability, and reducing rearing densities. General results from these studies are summarized below:

- 1) Survival of subyearling Chinook salmon is usually improved with NATURES enhancements that include camouflage covers, structure (suspended evergreen trees) and substrate. Of these, substrate may be the most important factor as it improves cryptic coloration of fish and thereby reduces predator detection.
- 2) Yearling Chinook and coho salmon survival is usually not improved with NATURES enhancements. Yearling smolts are silvery in color and exhibit rapid emigration compared to subyearling Chinook salmon.
- 3) Adult salmonid survival is enhanced when fish are reared in semi-natural earthen ponds versus concrete raceways, even when fish are placed in the pond for a short time prior to release.

Several studies have been conducted on the effects of the rearing environment on survival rates of steelhead and cutthroat smolts. An experiment was conducted at the Cowlitz Trout Hatchery to determine relative adult survivals to steelhead by adding structure to a semi-natural earthen pond (Tipping, unpublished). About 5,000 denuded evergreen trees were added to one 5-acre pond while a second similar pond was used as

a control. Similar numbers of fish were reared and released from both ponds and fish were released in 1996-1998. Adult fish recoveries were similar, 0.43% and 0.44% for control and NATURES fish, respectively.

An ongoing experiment at Marblemount Hatchery involves steelhead reared in an earthen pond while a second similar pond is asphalt lined (Tipping, unpublished). Adult returns from the first two of three releases were significantly greater for fish reared in the earthen pond than the asphalt pond. The 2-salt recoveries from the last release also had significantly more fish recovered from the earthen pond than the asphalt pond.

In an experiment at the Cowlitz Trout Hatchery, adult survival of sea-run cutthroat trout reared in a semi-natural rearing pond was 60% greater than that of fish reared in concrete raceways (Tipping 1998a). A subsequent study found fish placed in a semi-natural pond for four to seven months before release had 160% greater adult survival than raceway-reared fish, while fish reared for only one month in the semi-natural pond prior to release had 98% greater adult survival than raceway-reared fish (Tipping 2001a). So, even a one-month exposure to the pond environment nearly doubled adult survival. Possible reasons for the improved survival of semi-natural pond fish included 1) reduced rearing density; 2) reduced condition factor (K), which has been associated with migrating versus non-migrating steelhead smolts (Ewing et al. 1984; Tipping et al. 1995); 3) possible cryptic coloration differences which might help fish avoid predation (Donnelly and Whoriskey 1991; Maynard et al. 1995); and 4) increased exposure to natural feed organisms which thrive in mud bottoms and may help fish in post-release foraging ability (Savino et al. 1993; Maynard et al. 1996).

Regional and Temporal Trends in Survival Rates

We computed survival rates for a number of hatchery programs throughout the state to evaluate regional and temporal trends. In general, we attempted to select hatchery programs with consistent rearing methods and where estimates of the escapement were available. However, in most cases, the estimates are indices rather than survival rates as not all returning fish are enumerated. Also, in some cases, adults may be counted a second time after return to the hatchery, release to the river, and subsequent capture by an angler. Survival rates were typically computed by dividing the total return (all age classes) of hatchery-origin steelhead by the number of steelhead smolts released two years earlier. For example, smolts from the 1974 brood of winter steelhead were released in the spring of 1975 and predominantly contributed to catch in the winter of 1976-1977.

Datasets used in the analysis are summarized below:

Puget Sound. Winter steelhead smolt release, catch, escapement data were used from the Skagit River, the Elwha River, and the Puyallup River.

Olympic Peninsula. Winter steelhead smolt release, catch, escapement data were used from the Quillayute River and the Quinault River.

Southwest Washington. Winter steelhead smolt release, catch, and escapement data were used from the Humptulips River and the Elochoman River.

Lower Columbia River. Winter steelhead smolt release, catch, and escapement data were used from the Kalama River and the Washougal River. Summer steelhead smolt release, catch, and escapement data were used from the Kalama River.

Middle Columbia River. Survival rates were computed based on coded-wire-tag recoveries for steelhead released from the Touchet Acclimation Pond (WDFW 2005a)

Upper Columbia River. Survival rates were computed based on age specific returns to the Wells Hatchery (WDFW 2002a; C. Snow, pers. comm.).

Snake River. Survival rates were computed based on coded-wire-tag recoveries for steelhead released from the Lyons Ferry Hatchery (2005b).

Survival rates for juvenile steelhead released varied substantially between regions and years but some consistent patterns were evident (Fig. 3-2). Juveniles released from programs on the Olympic Peninsula (4.4% for 1995 through 1998 broods) and in Southwest Washington (3.3% for 1995 through 1998 broods) always had the highest survival rates. Survival rates for steelhead released from hatcheries in the Upper Columbia and Snake River programs were generally the lowest (< 1%). Perhaps most surprising, however, was the collapse in the survival rates for programs in Puget Sound. In the first 10 years of the analysis, the average survival rates for steelhead released from these programs was in the range of 3 to 4.5%. In the most recent four years, the average survival rate was 0.4%, the lowest of all regions in Washington.

The pattern in survival rates was similar for the winter steelhead programs in each of the three rivers in Puget Sound (Skagit River, Puyallup River, and Elwha River) (Fig. 3-3). Survival rates were variable but relatively high for the 1975 through 1981 broods, reaching a maximum of 7% on average for the 1982 brood. A precipitous decline in survival rates occurred subsequently and by the 1995 brood the average survival rate had dropped to 0.2%. Average survival rates have ranged from 0.2% to 0.5% since that time.

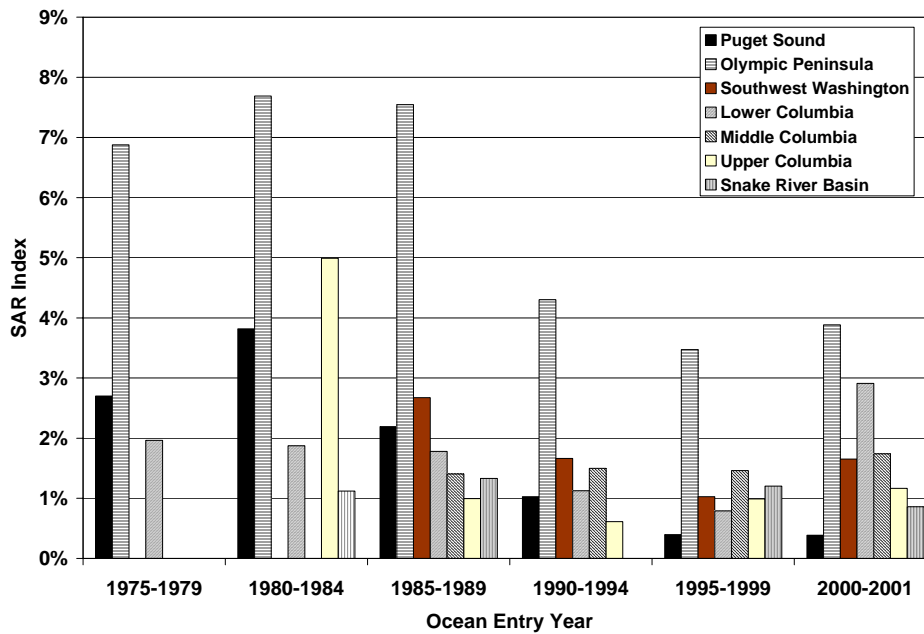


Figure 3-2. Average survival indices for steelhead released from artificial production programs in Washington.

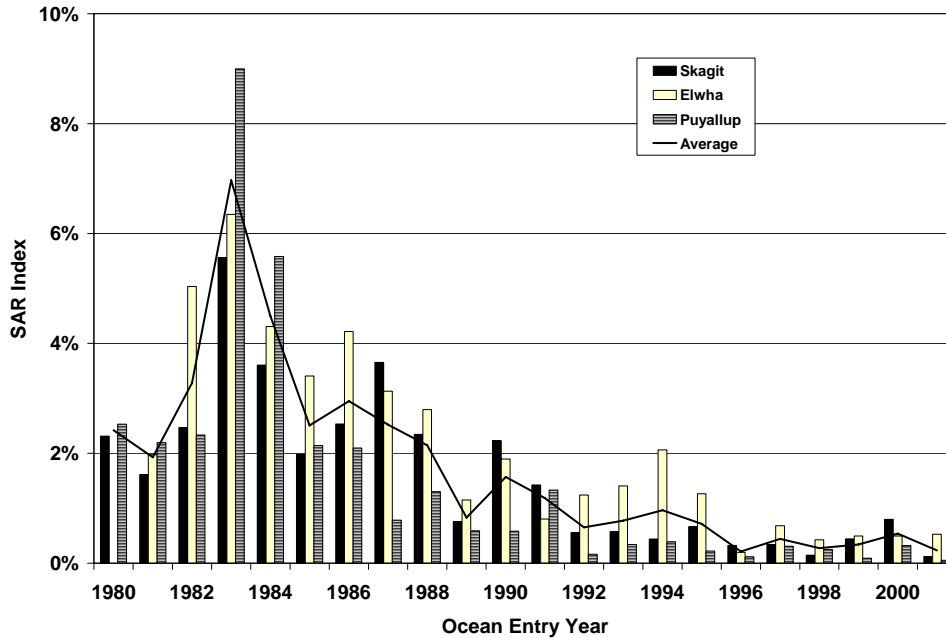


Figure 3-3. Survival rate indices for winter steelhead released from three artificial production programs in Puget Sound.

Although a number of hypotheses exist for the reduction in survival rates for the Puget Sound steelhead programs, the most likely explanation is a shift in oceanic conditions affecting early marine survival. Welch et al. (2000) found substantive declines after 1990 in survival rates for steelhead from rivers entering Georgia Strait, but no change or increased recruitment for steelhead from the west coast of Vancouver Island and northern British Columbia. Although the exact functional mechanism remains unknown, Welch et al. (2000) suggested that anomalous atmospheric circulation patterns in 1989 resulted in a sharp change in oceanic conditions and reductions in the survival rates for many stocks. Potential explanations for the reduction in survival rates for Puget Sound steelhead are discussed further in Chapter 7.

3.3 Genetic Effects on Natural Populations

Royal (1973) was perhaps the first to raise questions regarding the effectiveness of hatchery steelhead production programs in Washington and their potential impacts on natural steelhead populations. In response to such concerns for ecological and genetic risks of hatchery production on wild populations, research on fitness of hatchery fish spawning naturally and their interactions with wild stocks was initiated in the mid-1970s. Until recently, most research involved assessment of isolated hatchery stocks of non-local origin. Recently, there has been increased interest in integrated hatchery programs that use broodstock of local-origin. The risks and benefits of integrated versus isolated programs are discussed in this chapter and in Chapter 4, where tradeoffs are evaluated in concert with harvest management strategies and habitat productivity.

3.3.1 Overview of Genetic Risk

Genetic hazards posed to salmonid populations by hatchery operations fall into four main categories: 1) extinction, 2) loss of within population diversity, 3) outbreeding depression and loss of among-population diversity, and 4) domestication (Busack and Currens 1995). Extinction risk differs significantly from the others in that it typically has nongenetic causes, and is fairly easily controlled by good hatchery design, management, and equipment. The other three hazards are potential risk factors in all hatchery operations, though there is considerable uncertainty about the severity and permanence of their impacts (Busack and Currens 1995; Campton 1995).

Gene Flow between Hatchery-Origin and Natural-Origin Steelhead

To understand how steelhead programs in Washington may genetically affect natural populations and natural spawning components of composite populations, it is important first to have a clear conceptual picture of gene flow from hatchery-origin to natural-origin steelhead and vice versa. Fig. 3-4 shows all possible gene flow paths between a

group of hatchery fish and a natural spawning group. At this point, these can either be considered separate populations or two components of the same population (which is biologically more correct in many cases). The diagram shows the two spawning components of the population (or two populations) and four groups of fish. The smaller arrows show hatchery-origin fish spawning in the hatchery (called hatchery-origin broodstock [HOB]) and natural-origin fish spawning in the wild (called natural-origin spawners [NOS]). The larger arrows depict fish spawning in the environment opposite the one they came from: natural-origin fish spawning in the hatchery (called natural-origin broodstock [NOB]) and hatchery-origin fish spawning in the wild (called hatchery-origin spawners [HOS]). If a fish spawning in the hatchery doesn't come from the wild it must have come from the hatchery, and if a fish spawning in the wild doesn't come from the wild it must have come from the hatchery.

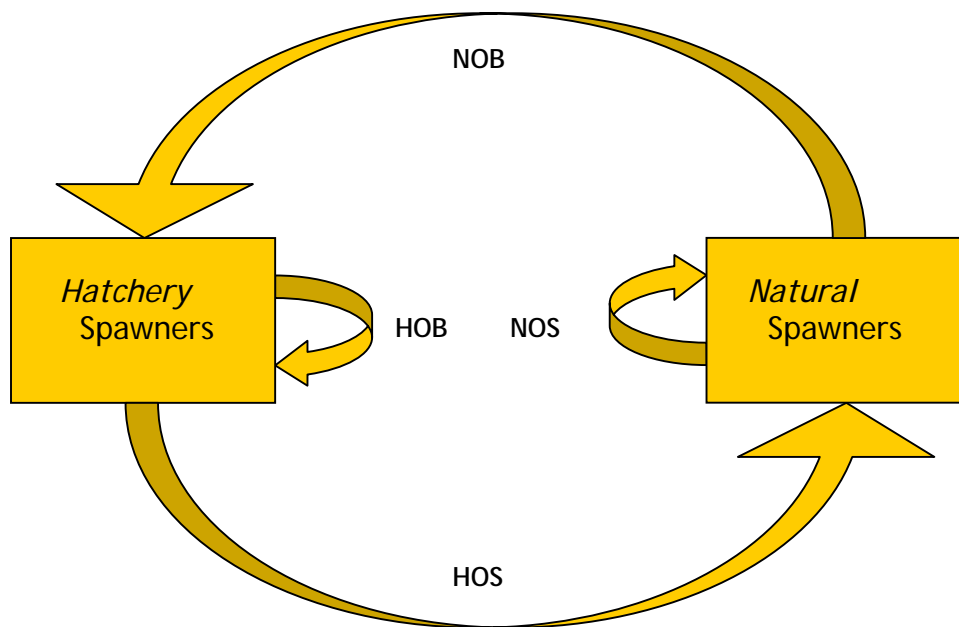


Figure 3-4. Schematic of reproductive interactions between natural and hatchery subpopulations in an integrated production program (from Lynch and O'Hely, 2001).

As discussed in section 3.2.1, hatchery programs use either an isolated or integrated reproductive strategy. In isolated programs, the intent is to keep hatchery and natural fish genetically separate. Gene flow is not desired, especially from hatchery to natural, as depicted in Fig. 3-5. The diagram clearly shows that spawning of the two groups is isolated. The dotted arrow represents unintentional gene flow from the hatchery population to the natural population. In isolated programs hatchery and natural fish are managed as two separate populations.

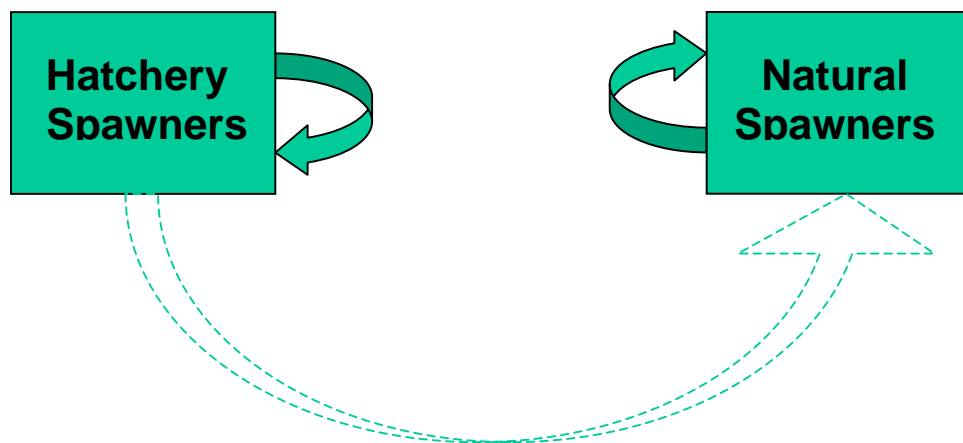


Figure 3-5. Schematic of a Isolated hatchery program interacting with a natural population. Dotted arrow represents low levels of gene flow.

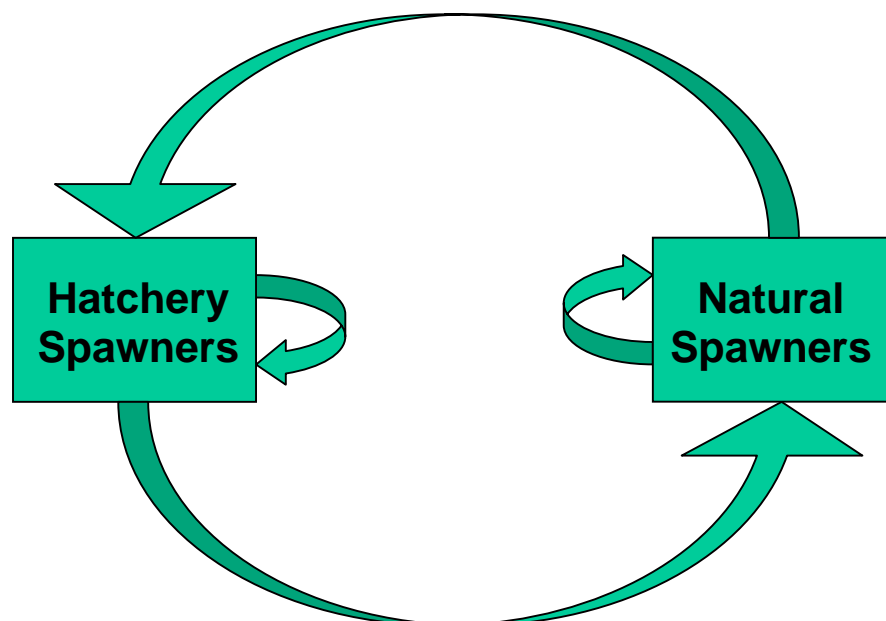


Figure 3-6. Schematic of an integrated hatchery program interacting with a natural population.

In integrated programs, interbreeding between the hatchery and natural fish, and vice versa, is intended (Fig. 3-6). This differs from the way many biologists and resource managers have traditionally thought about hatchery fish on the natural spawning grounds and prompts a refined definition of “stray”. In general, all hatchery fish on the natural spawning grounds were considered “stray” since they were not removed through harvest, nor returned to the hatchery of origin. Thus, although a program may have been in place for years with hatchery fish commonly spawning in the natural environment and perhaps some natural-origin fish contributing to the hatchery broodstock, the perception was there were two discrete populations. However, it is highly probable most of the natural-origin fish had at least one hatchery origin parent.

Modeling and initial genetic analysis suggest that even limited gene flow can unite the groups genetically. Therefore, in these situations, it’s better to view this as a single population that spawns in two environments rather than two populations. Genetic distinctions between the hatchery and natural origin fish when they commingle in spawning are often small and temporary, reflected mostly by the additional generation in the hatchery environment for hatchery fish. The situation could be compared with a single population that spawns in two streams.

Loss of Within-Population Diversity

Loss of within-population diversity in salmonid hatchery operations has been widely documented (Hindar et al. 1991). The causes are primarily sampling the population inadequately for inclusion as hatchery broodstock, using too few fish as broodstock, or a combination of the two. The result is that some genetic variation present in the source population is lost. Waples (1999) argues that loss of some diversity is inevitable.

Loss of within-population diversity is often determined by the effective size of the population. Effective size is one of the preeminent concepts in conservation biology. In a genetically ideal population, all parents have an equal probability of contributing to the next generation and there are equal numbers of males and females. The effective size of a population is the size of a genetically ideal population that loses genetic diversity at the same rate as a given population. Thus, in a genetically ideal population the effective size and census size is the same, but the more the sex ratio deviates from 1:1 and the more fish vary in reproductive potential, the smaller the effective size becomes relative to the census size. The expected loss of diversity per generation is $1/2N_e$, where N_e is the effective population size. Effective sizes of a few hundred to a few thousand are considered necessary for adequate conservation of genetic variability (Lande and Barrowclough 1987; Lande 1995). These analyses assume totally isolated populations, however. Gene flow can significantly increase the true effective size of a local population (Whitlock and Barton 1997; Tufto and Hindar 2003). Because of this phenomenon, the importance of effective size as a risk factor is under review by geneticists evaluating populations of salmon and steelhead in the Pacific Northwest.

Concerns about loss of variability due to sampling error, such as exclusion of life history types, remain.

A great concern in integrated hatchery programs, especially those used for conservation, is the Ryman-Laikre effect (Ryman and Laikre 1991, Ryman et al. 1995). Because survival of hatchery juveniles to adulthood is often considerably higher than that of natural-origin juveniles, the contributions of individual hatchery fish to the next generation can be considerably higher than the contributions of natural-origin fish, depressing effective size.

Outbreeding Depression and Loss of Among-Population Diversity

Outbreeding depression and loss of among-population diversity are considered a single hazard because they both result from gene flow among populations. Some gene flow among salmonid populations is natural and healthy, and is an important force in maintaining genetic diversity in populations. Estimates of gene flow are rarely available for natural populations of steelhead, but the percentage of spawners originating from nonlocal populations has occasionally been estimated. Shaplov and Taft (1954), for example, estimated that about 2% of the population in two small California streams originated from other streams.

A potential concern is that excessive gene flow from nonnative hatchery fish spawning with native natural-origin spawners will cause a loss of fitness called outbreeding depression (Templeton 1986; Emlen 1991; Roff 1997). Although outbreeding depression has recently been well demonstrated by hybridizing largemouth bass from neighboring states (Philipp et al. 2002), evidence in salmonids is scant. Bams (1976) demonstrated that hybrid pink salmon do not home to natal streams as well as pure local stock. Gharrett and Smoker (1991) found significant outbreeding depression in crosses of odd-year and even-year pink salmon and their work is often cited as evidence of outbreeding depression. However, these two groups of pink salmon for all practical purposes are distinct species. Most of the concern about outbreeding depression in salmonids is indirect, based on the vast amount of local adaptation that seems evident (Taylor 1991). Reisenbichler (1988), for example, showed that the return rate success of coho salmon varied inversely with the distance between release point and hatchery of origin. A NOAA Fisheries- sponsored workshop on the effects of gene flow through straying was held at Seattle in 1995 (NMFS 1997). The conclusion of the panel, based on outbreeding depression arguments, was that significant losses might occur at gene flow rates (measured as proportion of recipient population) less than 5%, so that rates as high as 5% are not justifiable.

The concern about gene flow may seem odd because of the common public perception, based on agriculture, that hybridization is a positive thing. It is important to consider that plants and animals under, in many cases, centuries of culture are quite inbred, so

the phenomenon of “hybrid” vigor is not surprising because the hybridization causes a large increase in genetic variability in the population. There is little, if any, evidence of hybrid vigor in crosses of natural animal populations.

The above material treats gene flow from only one perspective, that of its ability to reduce fitness. There is another more subtle risk posed by gene flow from exogenous sources, that of loss of *among-population* diversity. If two locally adapted populations exchange genes, they will both have increased levels of within-population diversity, but the genetic differences between them will decrease, so among-population diversity is decreased. This is a loss in biodiversity whether or not there is a fitness consequence to the interbreeding.

Domestication

Domestication is the adaptation of organisms to anthropogenic environmental changes. In hatcheries, the concern is that fish will become genetically more adapted to the hatchery “lifestyle” of incubation and early rearing in the hatchery followed by later life in the wild and less adapted to the purely wild life. This will be true not only of “hatchery stocks” but also true to a more limited extent of “natural stocks” with which hatchery fish regularly interbreed or into which they stray. This is probably the single most controversial and least understood topic in the general debate about hatchery risk. For this reason, the theory behind the concern requires some careful explanation.

Our prevailing model of natural selection is that the environment is constantly working to genetically refine an organism. Thus, we consider wild fish to have become well adapted to their environments. If we spawn and rear fish in the hatchery for part of their lives, for that portion of their lives they will experience a much different set of selection pressures than they would in the wild. The hatchery-reared progeny of wild fish taken into the hatchery for broodstock can be expected to differ genetically slightly from their parents. If these fish return as adults and are themselves used as broodstock, their progeny will differ slightly genetically from them, and so on, each generation changing slightly in the direction that the selective forces imposed by the hatchery environment. If hatchery fish sometimes spawn in the hatchery and sometimes in the wild, the proportionate selective effects of the hatchery and natural environments will determine how much the population changes (Ford 2002; Lynch and O’Hely 2001).

There are three popular arguments for the viewpoint that domestication should not be a real concern in salmonid hatchery programs. First, that hatchery programs relax selection more than they change selection regimes. For example, the hatchery provides a much less selective incubation environment than the wild. Theorists would agree, but this relaxation is part of domestication, and in theory can cause considerable genetic change (Lynch and O’Hely 2001). Second, that hatcheries can’t be selective because

survival rates of juveniles from the hatchery are so high. While it is true, that the high juvenile survival rates do occur, in all salmonid populations a huge percentage of the fish die before they get a chance to spawn. If the survivors are a different genetic mix than they would have been had they not been produced by the hatchery, then domestication has occurred. Third, that releasing the fish into the wild counteracts any selection that might have occurred in the hatchery. This may happen to some extent, but there is scientifically no basis for expecting it to cancel out the hatchery effects.

Empirical evidence for domestication in salmonids is abundant. Berejikian and Ford (2004) comprehensively reviewed both published and unpublished information regarding the relative fitness of hatchery and natural salmon and steelhead. Much of the relative fitness work that has been done has been conducted on steelhead, and mostly in Washington and Oregon. The majority of the studies compared the natural reproductive success (measured as offspring produced per spawner) of transplanted (non-local origin) hatchery stocks to that of natural-origin fish spawning in the same streams (Leider et al. 1990; Hulett et al. 1996; Blouin 2003; Kostow et al. 2003; McLean et al. 2003, 2004). One study in Oregon (Blouin 2003) also compared the reproductive success of hatchery and natural-origin steelhead when the hatchery stock was spawned from a local natural stock.

Some of the data from these studies are summarized in Table 3-3, organized relative to the type of broodstock.

Domesticated, Nonlocal Broodstock

The summer steelhead studies conducted with domesticated broodstock each involve a derivative of the Skamania hatchery stock. Fitness is compared to three natural populations: 1) Kalama River summer steelhead (Leider et al. 1990); 2) Clackamas River (Oregon) winter steelhead (Kostow et al. 2003); or 3) Hood River (Oregon) summer steelhead (Blouin 2003).

Two of the studies of domesticated stocks of winter steelhead involve a derivative of the Chambers Creek stock: 1) Beaver Creek Hatchery stock (Chambers Creek origin) compared to the Kalama winter-population (Hulett et al. 1996); and 2) the Bogachiel Hatchery stock (Chambers Creek origin) compared to the winter-run steelhead of natural-origin in Forks Creek (Willapa River) (McLean et al. 2003, 2004). The third domesticated winter-run stock studied was the Big Creek Hatchery (Oregon) stock (Lower Columbia origin) compared to the natural, winter-run population in the Hood River (Blouin 2003).

Collectively, the available data convincingly demonstrate that the reproductive success of domesticated, non-locally derived hatchery steelhead stocks is likely to be low relative to natural-origin spawners in the same streams (Table 3-3). In the summer

steelhead studies, the hatchery spawners averaged only 28-30% as many smolt offspring and 9-37% as many adult offspring as did the natural-origin spawners. Findings from the winter steelhead studies were qualitatively similar. Relative reproductive success to the smolt stage was low (4-7% of that of natural-origin fish) in Forks Creek, but was higher and much more variable in the Kalama study. Hatchery-origin adults produced an estimated 284% as many smolts as natural-origin adults in the Kalama one brood year, but only 33% and 61% as many as natural-origin adults the other two years. Relative reproductive success to the adult stage was low in both the Kalama and Forks Creek studies (hatchery adults averaged 7-8% as productive as natural-origin adults), and somewhat higher (34% of that of natural-origin adults) in the Hood River study.

Table 3-3. Reproductive success estimates of hatchery steelhead spawning in natural streams in the presence of natural-origin steelhead. Relative fitness is expressed as the number of offspring per hatchery spawner divided by that of the natural-origin spawners, for the smolt and returning adult stages of naturally produced offspring.

Location	Relative Fitness		Citation
	Smolts	Adults	
<i>Summer Steelhead, Domesticated, Nonlocal Broodstock</i>			
Kalama River Washington	0.30 (0.12-0.53)	0.16 (0.12-0.21)	Leider et al. (1990) ¹
Clackamas River Oregon	0.28 (0.18-0.37)	0.09 (0.04-0.13)	Kostow et al. 2003)
Hood River Oregon	NA	0.37 (0.17-0.54)	Blouin (2003)
<i>Winter Steelhead, Domesticated, Nonlocal Broodstock</i>			
Kalama River Washington	1.26 (0.33-2.84)	0.08 (0.0-0.21)	Hulett et al. (1996) ¹
Forks Creek Washington	0.06 (0.04-0.07)	0.07 (0.02-0.11)	McLean et al. (2003) McLean et al. (2004)
Hood River Oregon	NA	0.34	Blouin (2003)
<i>Winter Steelhead, Local Natural-Origin Broodstock</i>			
Hood River Oregon	NA	0.91 (0.85-1.08)	Blouin (2003)

¹ The data presented here for the two Kalama studies differ somewhat from those reported in Leider et al. (1990) and Hulett et al. (1996) because of unpublished changes in methods to calculate reproductive success. These changes include elimination of the Leider et al. (1990) procedure to standardize production to potential egg deposition, instead estimating production on a per spawner basis (consistent with other studies reported here). The earlier published data and those provided here lead to the same conclusions.

Natural Origin, Local Broodstock

The Hood River study (Blouin 2003) is the only one to have reported lifetime (adult to adult) reproductive success of first generation hatchery steelhead spawned from local, natural-origin broodstock compared to natural-origin spawners of the same stock (Table 3-3). Averaging male and female success across the three brood years (1996-1998), the hatchery adults produced 91% as many adult offspring as did the natural-origin adults (per spawner). Individual brood year values ranged from 85-108% for females and 85-90% for males.

At least two studies shed light on the fitness of hatchery stocks that were founded with wild spawners but had more than one generation of hatchery production spawned from returning hatchery adults. Reisenbichler and McIntyre (1977) conducted controlled crosses of wild adults and hatchery adults that had been cultured for two generations since being founded by wild fish in the Deschutes River, Oregon. Relative survival of embryos stocked in streams from hatchery crosses was 91% of that of wild crosses to the emergence stage, 81% to age-0, and 79% to age-1. Intermediate survival was observed from hybrid crosses of hatchery females spawned with wild males (92%, 85% and 87% to emergent fry, age-0 and age-1, respectively). In parallel experiments conducted in a hatchery environment, the hatchery offspring survived better. Because of the controlled nature of the experiment, these results are regarded as representing genetic differences not confounded by environmental effects. However, there are no data on the survival of the experimental fish beyond age-1, so the lifetime fitness under this scenario is unknown.

Preliminary data from another local origin, multi-generation hatchery stock are available from a study conducted on Little Sheep Creek in NE Oregon (Moran, pers. comm.). As reported by Berejikian and Ford (2004), Moran found that naturally spawning hatchery females produced about 40% as many parr offspring as did natural females and 33% as many parr as natural males.

Other Studies

In other species, apparent effects of domestication have been noted in reproductive success (Fleming and Gross 1992; Fleming and Gross 1993; Petersson and Jarvi 1993), morphology (Fleming and Gross 1989; Hard et al. 2000; Swain et al. 1991; Taylor 1986), agonistic behavior (Berejikian et al. 1996; Swain and Riddell 1991), and assorted life-history traits (Kallio-Nyberg and Koljonen 1997; Petersson et al. 1996).

The literature, although plentiful, leaves a lot to be desired. Most domestication studies involve comparisons of populations that have had heavy hatchery impacts with those that have not, so there is always the possibility of differences between populations not related to hatchery rearing being confused with domestication. Many studies also don't clearly distinguish between phenotypic effects of hatcheries,

differences that may be caused solely by the fish being reared in a hatchery and that may be nongenetic, and true genetic differences. Most importantly for the discussion in the next section, virtually no research has been done on integrated programs, programs in which there is substantial gene flow between the hatchery and natural components of the population. Therefore, important questions as to the severity and permanence of domestication impacts and our ability to reduce impacts remain unanswered (Busack and Currens 1995; Campton 1995). However, echoing Busack and Currens (1995), we are unaware of any study looking for domestication that did not find it. The combination of evidence and theory make a compelling case for domestication being a concern in populations affected by hatchery operations. A number of regional scientific panels have underscored these concerns (e.g. Independent Scientific Advisory Board (ISAB) 2003; Independent Multidisciplinary Science Team (IMST) 2001).

3.3.2 Genetic Risks of Isolated Hatchery Programs

As stated earlier, in an isolated program the hatchery fish and the natural fish with which they may interact are considered two separate populations. Limiting interactions between the two groups controls the risks of these programs. In practical terms this means limiting gene flow from the hatchery-origin fish into the natural spawners, and limiting the ecological interactions between the two.

The gene flow issue is both a domestication risk and an outbreeding depression/loss of among population diversity risk. Both problems stem from the stock used for the hatchery releases, which is invariably domesticated and typically of nonlocal origin. Isolated steelhead programs often involve release of fish from a small number of centralized hatchery stocks, typically Chambers Creek winter steelhead, Skamania summer steelhead, and localized derivatives of the one of the two. The localized derivatives may have some additional ancestry from other populations, but the essential feature of these stocks is a long history of domestication directed at producing a one-year smolt (Crawford 1979). Thus, not only have the fish been subjected to generalized domestication, there has been artificial selection for early run-timing and spawning. Except for the occasional inclusion of wild fish, these are closed populations that do not spawn in the wild. Thus, the push-pull of hatchery and natural selective forces has been strongly in the hatchery direction. It is reasonable to assume these fish have been heavily domesticated for 50 years.

The Chambers Creek stock originated in south Puget Sound, and the Skamania stock originated in the lower Columbia (Crawford 1979). These two stocks and their local derivatives (e.g. Bogachiel) are widely planted all over western Washington, especially the Chambers Creek stock. They are almost always nonnative fish where they are planted. Thus, in addition to the domesticating effect of gene flow from a highly

domesticated source, isolated programs include a risk of outbreeding depression/loss of among-population diversity. The risk varies with the degree of nonlocality and with the possible local adaptation that the domesticated stock may have developed. For example, there is more outbreeding depression risk from Chambers Creek stock released into north coastal streams than there would be from Chambers Creek stock released into a Puget Sound tributary. However, there would be less outbreeding depression risk from the Bogachiel derivative of the Chambers Creek stock being released into a north coastal stream than Chambers Creek stock from a Puget Sound hatchery, because the Bogachiel stock has had time to develop some level of local adaptation.

The risk due to this gene flow depends on the domestication level of the stock used, the degree of nonlocality of the stock used, the level of gene flow the population has already undergone (a stock that has already had a certain level of gene flow will be less impacted incrementally than one that has had less), and the level of gene flow. Gene flow depends on the relative abundance of hatchery and wild spawners on the spawning ground, their temporal and spatial overlap, and the relative success of the three types of matings (hatchery x hatchery [HxH], hatchery x natural [HxN], and natural x natural [NxN]). Fig. 3-7 shows the situation with regard to mating structure. There are three regions on the figure, each representing a different mating scenario. In region A, only hatchery-origin fish are present, so only HxH matings take place.

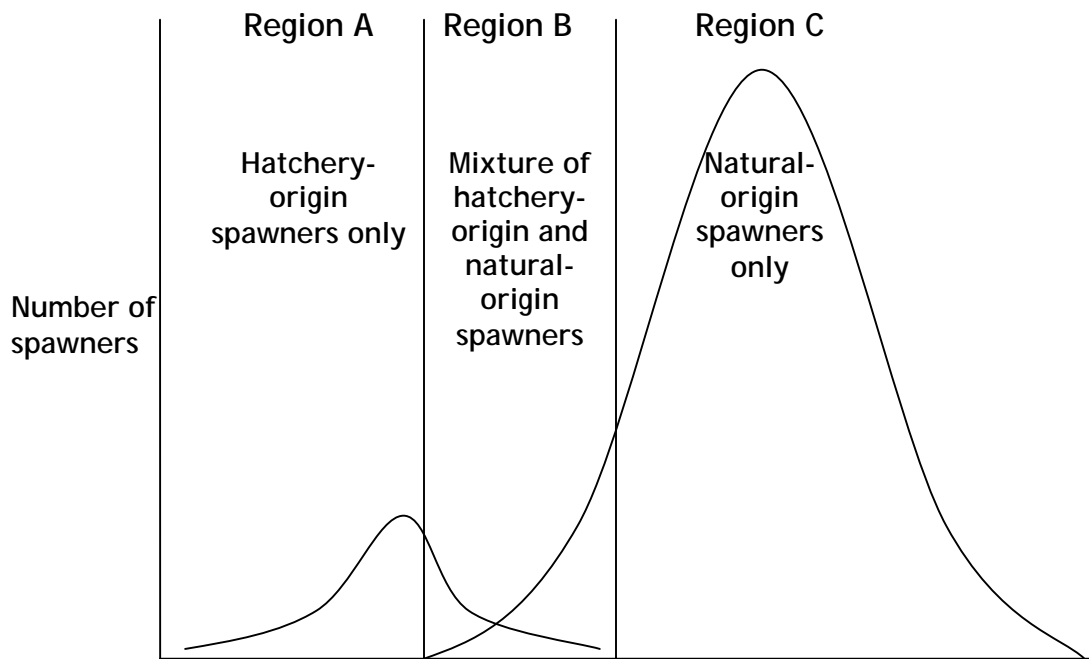


Figure 3-7. Schematic of temporal spawning overlap between early-run hatchery-origin winter steelhead and natural-origin winter steelhead. The shape, sizes, and placement of curves does not represent any particular real situation.

In region C, only natural fish are present, so all matings are NxN. In region B, both types of spawners are present. Assuming fish mate at random and assuming single-pair mating, there will be p^2 HxH matings, $2p(1-p)$ HxN matings, and $(1-p)^2$ NxN matings, where p is the proportion of hatchery-origin fish present in region B. For example, if during the time the two runs overlap the proportion of hatchery-origin fish is 10%, the expected frequency of the three types of matings will be 1% HxH, 18% HxN, and 81% NxN.

The level of gene flow to be expected from the scenario depicted in Fig. 3-7 is (see also derivation in Appendix 3-A):

$$\text{Gene flow} = \frac{b}{b + a(1 - q)(1 - o_N) + (1 - q)^2 o_N^2}, \text{ where}$$

$$a = o_N + q(o_H - o_N)$$

$$b = k_1(aq(1 - o_H) + q^2 o_H^2) + k_2 q(1 - q)o_N o_H$$

and k_1 and k_2 are the fitnesses of HxH and HxN matings relative to NxN, respectively; q is the proportion of hatchery fish among all spawners (regardless of overlap), o_h is the proportion of the hatchery spawners that are in the overlap region, and o_n is the proportion of the natural-origin spawners that are in the overlap region. For example, assume 1) there are 150 natural-origin spawners, and 20 hatchery-origin spawners present; 2) 10% of the natural-origin spawners overlap with 5% of the hatchery-origin spawners; and 3) the fitnesses of HxH and HxN matings relative to NxN are 0.5 and 0.75, respectively. Here $q=20/170=0.118$, $o_H=0.05$, $o_N=0.1$, $k_1=0.5$, and $k_2=0.75$, so the gene flow is 6.4%.

Note that the expected gene flow rate can be much lower than the “stray” rate. In a well run isolated program, the level of gene flow should be quite low for three reasons: 1) the numbers of hatchery-origin fish that have escaped harvest should be low compared to the number of natural-origin fish present; 2) the reproductive success of the hatchery-origin fish can be expected to be low (Leider et al. 1990; Kostow et al. 2003; McLean et al. 2003; McLean et al. 2004); and 3) spawning overlap may be low.

As previously mentioned, there is no consensus on the impacts of gene flow from non-native sources (NMFS 1997). There is also no way to predict the impact of doses of domestication delivered this way, although some insights might be gained by contrasting this discussion with the discussion of integrated programs below. We can make some predictions based on basic population genetic theory of the balance between selection and migration. The genetic material in a population is maintained by selection

coefficients, symbolized by s . The selection coefficients can basically be thought of as defending the population from the inflow of nonadaptive genetic material. The basic idea is that if the gene flow rate (also called migration rate) exceeds the selection coefficient, the immigrant genetic material will over time replace the native material (NMFS 1997). Selection coefficients in nature for single traits are thought to be low (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001),

It does not take much migration to replace native (or less domesticated) genetic material with immigrant genetic material. Because we really don't know what the selection coefficients are, a detailed analysis using a variety of selection coefficients is not much more informative than the general statements just presented. It is important to gain some sense of how fast this replacement can take place. For varying levels of constant gene flow, the rate at which the genetic difference between a donor and recipient population decreases for selectively neutral genetic material (i.e., that is not selected against) is given by:

$$\text{Decrease in Genetic Difference} = 1 - (1 - m)^t$$

where m is gene flow and t is generations (Hedrick 1983). Examples of this kind of variation are the neutral protein and DNA markers that are used to describe differences among fish populations. With a gene flow rate of 2% for 14 generations (~50 yr), about 25% of the difference will be lost (Fig. 3-8). This graph represents the maximum rate at which native genetic material can be replaced by immigrant material. Genetic differences under selection will decrease more slowly, but those under low levels of selection (which may be quite common) will decrease almost as rapidly. This forms the basis of the general findings of the 1995 straying workshop (NMFS 1997), and the general guideline of the Hatchery Scientific Review Group (HSRG) that the stray rate of hatchery-origin fish onto the spawning grounds should not exceed 5% (HSRG, WDFW, and NWIFC 2004).

The decay of genetic differences between the hatchery stock and natural populations impacted by isolated programs may be of interest in its own right as a loss of among-population diversity, but the impact on current fitness is more relevant to immediate management and stewardship concerns. There is no way at present, to quantify the risk to fitness over either the long- or short term.

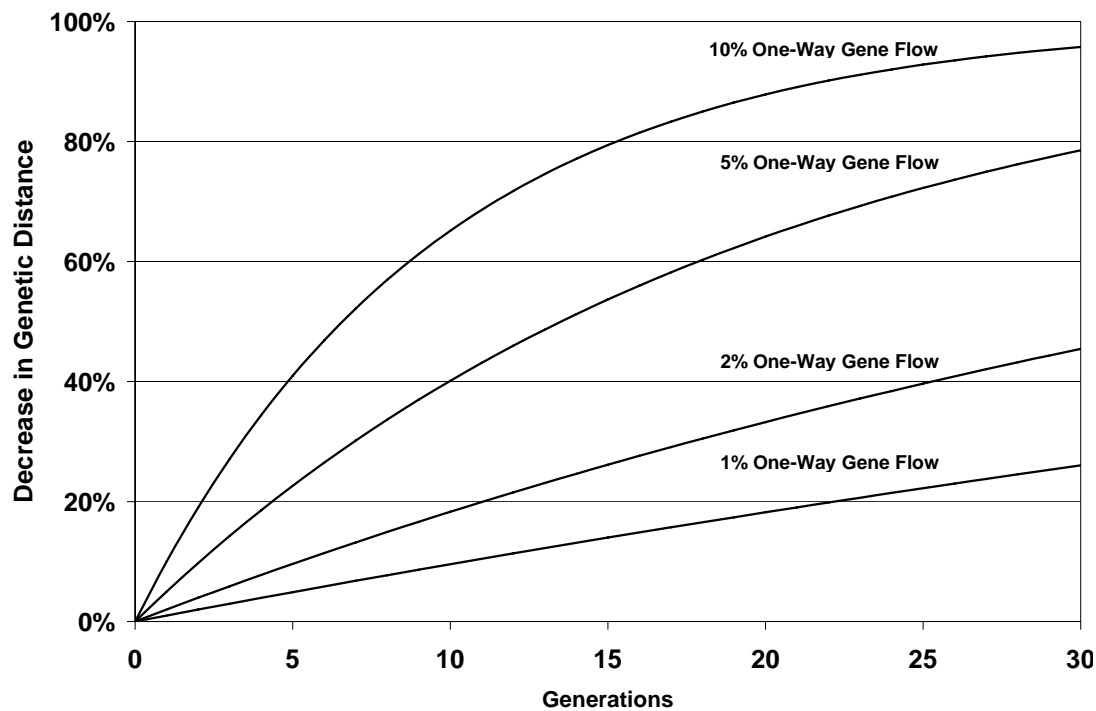


Figure 3-8. Decay of selectively neutral genetic differences between a donor and recipient population under varying levels of one-way gene flow

3.3.3 Genetic Risks of Integrated Programs

There are few integrated steelhead hatchery programs in Washington. Some began from native stock, others from conversion of isolated programs using mixed somewhat nonlocal stocks. Because hatchery-origin and natural-origin fish are managed as a single population in an integrated program (which indeed they are), these programs avoid the ecological-genetic risks discussed above for isolated programs. The major genetic risk in integrated programs is domestication, but there is also risk of outbreeding depression/loss of among population diversity if the program is begun with nonnative hatchery fish. As we saw in the discussion of isolated programs using nonnative hatchery fish, insufficient information exists to predict how much fitness loss will be suffered due to the introduction of nonnative genetic material. This risk can be minimized, however, by avoiding use of a distantly related hatchery stock, and by ceasing use of the nonnative stock as soon as possible.

Recent work on domestication by regional scientists has developed theory that helps a great deal in understanding the risk and in developing risk containment measures.

Integrated programs involve regular gene flow from the hatchery into the natural spawning component, and from the natural spawning component into the hatchery (Fig. 3-6). The domestication risk depends largely on these two levels of gene flow, and risk containment almost always requires regulating them. The key is a concept called *proportionate natural influence* (PNI). This concept is based on modeling by Lynch and O'Hely (2001). Mathematically,

$$PNI = \frac{pNOB}{pNOB + pHOS}$$

where *pNOB* is the proportion of natural-origin fish in the hatchery broodstock and *pHOS* is the proportion of hatchery-origin fish on the spawning grounds. The concept involves the assumption that these proportions are constant over time. Real programs, obviously, will vary, so these proportions can be thought of as means. Biologically, PNI is a measure of the proportion of time the population spawns in the wild, where it is subjected entirely to natural forces. Not at all obvious from this equation is the fact that any given PNI value represents a particular *pNOB/pHOS* ratio. For example, a PNI of 50% (.5) is achieved when *pNOB/pHOS* = 1 (i.e., when the proportion of natural-origin fish in the broodstock is the same as the proportion of hatchery-origin fish spawning in the wild. A PNI of 60% (or 0.6) is achieved when *pNOB/pHOS* = 1.5.

The idea of taking natural-origin fish into the hatchery to control domestication may seem counterintuitive. Biologists concerned with limiting the effects of hatcheries on natural production are accustomed to trying to keep natural-origin fish out of the hatchery, so the idea of putting them into the hatchery in a big way may seem like lunacy, but it makes sense genetically. Putting natural-origin fish into the hatchery retards domestication because the hatchery environment can't affect natural-origin fish as effectively as it can hatchery-origin fish. Keeping them out, and at the same time allowing hatchery-origin fish to spawn in the wild in large numbers actually makes domestication work faster.

The PNI concept can be displayed to good advantage on a "NOB-HOS" diagram (Fig. 3-9). This is a powerful diagram, both conceptually and practically. The triangular region below the 50% line represents combinations of *pNOB* and *pHOS* that result in PNI values greater than 50%. The triangular region to the left of the 50% represents combinations of *pNOB* and *pHOS* that result in PNI values less than 50%. With this graph you can see at a glance (without calculations) the kinds of *pNOB/pHOS* ratios that would be needed for any specified PNI. This graph can also be used to track programs. Any integrated program can be plotted on this graph if the *pNOB* and *pHOS* values can be estimated with reasonable accuracy; averages can be plotted, or the program can be plotted year to year. Programs can also be characterized by PNI value alone. Any integrated

program will have a PNI value between 0 and 1, and the PNI obviously tells you immediately the proportionate natural influence.

PNI, as might be expected, has a direct relationship to domestication, as illustrated by a model by Ford (2002). This model considers the change in a single trait (such as fecundity) in a population as it goes from being wild to being part of an integrated hatchery program. As explained earlier, in such a population, natural selective forces are pushing the population's traits toward the natural optimum, but hatchery selective forces are trying to pull the traits toward a hatchery optimum. The hatchery optimum is the trait value the population would eventually go to if it were never allowed to spawn in the wild. What the Ford (2002) model tells us is that at equilibrium, under assumptions of equal heritabilities and selection pressures in the natural and hatchery environments, the trait value on the line between the hatchery optimum and wild optimum is the PNI. A PNI of more than 50% leads to the population reaching an equilibrium state where its characteristics are more like those of a pure natural population than a pure hatchery population in that setting.

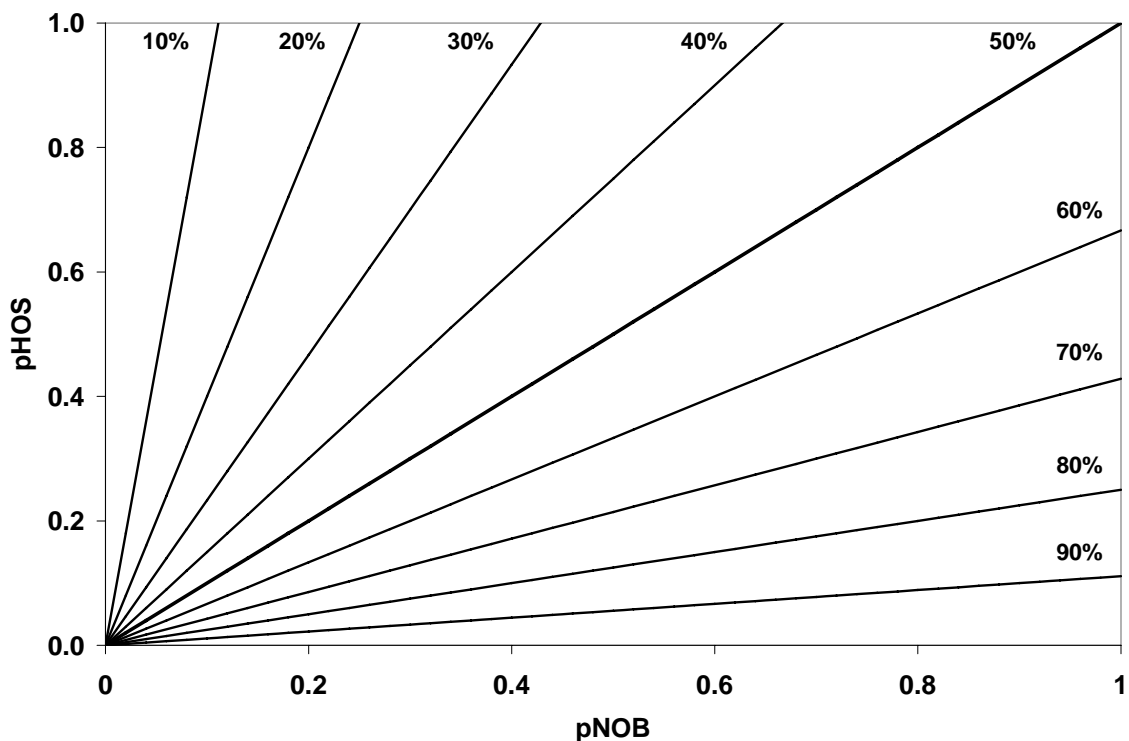


Figure 3-9. Proportionate natural influence in integrated hatchery programs as a function of pNOB and pHOS.

PNI is one important component of domestication risk. The other is the selective intensity of the hatchery environment; i.e., how it differs from the natural environment. For a given hatchery program, and given PNI, the genetic change the population undergoes will depend on this difference in environments. Thus, even with genetically conservative PNI values, making the hatchery environment more like the wild environment can lessen domestication. This means that hatchery operation modifications that make hatchery fish morphologically, behaviorally, and physiologically similar to wild fish may pay off in terms of lessening domestication.

Although we can use the PNI principle in concept to get some idea of relative risk of different programs, there is still much that we don't know biologically. Throughout this discussion we have treated domestication as if it were a single trait. It is several interacting traits, and we don't have an understanding of the exact genetic mechanisms behind them. Most importantly, we don't understand the relationship between PNI and fitness. The relationship between a change in trait mean and change in fitness is nonlinear. The actual fitness loss depends on the intensity of selection and how far the trait is moved from its wild optimum, neither of which is apparent from PNI.

3.3.4 Comparison of Genetic Risks of Isolated and Integrated Programs

Isolated and integrated hatchery programs can be evaluated relative to the risks they pose to among-population diversity and domestication. The fundamental distinction between a typical isolated program using a nonlocal hatchery stock and an integrated program using native stock is that the first involves low levels of gene flow from a highly domesticated and nonlocally adapted source into an otherwise "wild" stock, whereas the other deliberately puts the population through a program of adaptation to a mixed hatchery-natural environment. Programs using nonlocal stock potentially pose a risk to among-population diversity because of the different geographical origins of the two stocks; programs using local stock do not pose this type of risk. Thus, isolated programs, as currently operated with nonlocal stocks potentially pose a type of biodiversity risk that integrated programs based on a local stock do not.

The contrast between isolated and integrated programs in terms of domestication impacts can be stated quite simply. Well run isolated programs involve minor levels of gene flow from highly domesticated sources, whereas well run integrated programs involve higher levels of gene flow from less domesticated sources. Simplifying the difference in program types in this way suggests it may be possible to model the relative fitness impacts of the program types using the model of Ford (2002).

Ford (2002) evaluated quantitative genetic change at a single trait in populations with gene flow from hatchery to natural component and from natural component to hatchery

component using a simple model based on Lande (1976) and Bulmer (1985). Under this model, the mean of the trait in the natural component is given as

$$\bar{z}'_w = p_w \left\{ \bar{z}_w + \left[\frac{\bar{z}_w \omega_w^2 + \theta_w \sigma^2}{\omega_w^2 + \sigma^2} - \bar{z}_w \right] h^2 \right\} + (1 - p_w) \left\{ \bar{z}_c + \left[\frac{\bar{z}_c \omega_w^2 + \theta_w \sigma^2}{\omega_w^2 + \sigma^2} - \bar{z}_c \right] h^2 \right\},$$

the mean of the trait at time $t+1$ in the hatchery component is

$$\bar{z}'_c = p_c \left\{ \bar{z}_c + \left[\frac{\bar{z}_c \omega_c^2 + \theta_c \sigma^2}{\omega_c^2 + \sigma^2} - \bar{z}_c \right] h^2 \right\} + (1 - p_c) \left\{ \bar{z}_w + \left[\frac{\bar{z}_w \omega_c^2 + \theta_c \sigma^2}{\omega_c^2 + \sigma^2} - \bar{z}_w \right] h^2 \right\},$$

where the \bar{z} values are trait means in the natural (w) and hatchery (c) components of the population in generation t , and the \bar{z}' values are the corresponding trait means in generation $t+1$, p_w and p_c are the proportions of the fish that originated in the natural or hatchery environment, the ω values are the range of trait values with high fitness, the θ values are trait optima in the two environments, σ^2 is the phenotypic variance of the trait, and h^2 is the heritability of the trait. Note that the value of θ in the hatchery environment may be affected by cultural practices (e.g., natural rearing channels versus standard concrete raceways).

The relative mean fitness of a population component in a particular environment is given by

$$\bar{W} \propto \exp \left(\frac{-(\bar{z} - \theta)^2}{2(\omega^2 + \sigma^2)} \right)$$

(Lande 1976).

There are a number of assumptions inherent in use of the Ford model in general, and in this form:

- 1) that selection actually operates in this way, moving the population toward optima rather than simply directionally;
- 2) that trait values are normally distributed;
- 3) that the heritability is the same in the two environments;
- 4) that the genetic change does not involve loss of genetic material (change is completely reversible).

In using the Ford model to evaluate the fitness loss potential of typical nonnative stock segregated hatchery programs relative to integrated native stock programs, we made a

number of additional simplifying assumptions, similar to assumptions made by Busack et al. (2005):

- 5) it is reasonable for our purposes here to model domestication, which is actually a composite of many correlated traits, possibly with widely differing heritabilities, as a single trait with heritability 0.5
- 6) ω is the same in the two environments
- 7) using the above equations without incorporation of demographic features does not appreciably distort results.

We modeled typical segregated programs by use of the equations above, setting p_c to 1.0, and varying p_w from 0.98 to 0.80, which corresponds to gene flow from returning hatchery-origin fish into the natural spawning population of 2 to 20%. We assumed strength of selection (ω), expressed as standard deviation units, could vary from 2σ to 3σ , based on Hard (2004). For assumptions about the distance in optima between natural production and the domesticated hatchery stocks, we attempted to calibrate using the Forks Creek data of McLean et al. (2003; 2004), in which the relative fitness of the hatchery stock in the wild was 0.07, and the Hood River data of Blouin (2003), in which the relative fitness of the hatchery stock in the wild was 0.37 (see section 3.3.1 for a discussion of these studies). For each study we found the optimum value, assuming strength of selection of 2σ and 3σ that would yield the empirically observed fitness. Finally, we considered that despite several years of domestication, that the hatchery stock may have not reached its optimum, so modeled it at 0.33, 0.67, and 1.0 of its optimum, but ended up deciding this was too minor a factor to include so we modeled the hatchery stocks at their optima. Finally, we used fitness in the wild of the natural component after 20 generations as the simulation endpoint.

In modeling integrated programs we set p_c to 0.5 and varied p_w to simulate a proportionate natural influence (PNIs) of 0.5. We assumed the same range of strength of selection and range of optima as in the segregated modeling, but assumed that the integrated program could have a hatchery optimum that is considerably lower than a corresponding segregated program. We simulated programs with 25%, 50%, 75%, and 100% of the difference in optima not nearly as a much less distant from the natural optimum. In simpler terms, we considered that culture practices in a same-stock integrated program may be only 25%, 50%, or 75% as domesticating as the culture practices that created the Chambers Creek stock, as well as considering that they might be just as domesticating.

We summarized results as integrated/segregated fitness indices. The indices are ranges of fitness under integrated programs divided by the fitness under corresponding (same ranges of strength of selection and optima) isolated programs. The indices are presented in Fig. 3-10. The figure is divided into four panels, each representing a

different level of hatchery optima in the integrated program relative to the isolated program, and the levels are (from left to right) 25%, 50%, 75%, and 100%. Consider the results depicted in the 25% panel (far left). Results here assume that the hatchery optimum realized in the integrated program is 25% as distant from the original wild optimum as the hatchery optimum in a isolated program. A level of 1 on the y-axis (marked with a dark dotted line) indicates the point at which isolated programs conserve fitness as well as integrated programs. Above a level of 1, isolated programs do better at conserving fitness than integrated programs, and below they do worse. In the first (25%) panel we see then that segregated programs with a 2% gene flow rate can do almost as well (~96-99%) in conserving fitness as integrated programs, but isolated programs with gene flow rates of 20% do considerably worse (20-67%).

Three overall patterns are very clear from the figure. First, in general, integrated programs are generally better at conserving fitness than isolated programs, but isolated programs with low gene flow levels can be nearly as good or better. Second, the relative advantage of integrated programs over isolated programs depends on how domesticating the integrated program are. The 100% panel shows that if the integrated program is just as domesticating as the isolated program is, an isolated program may actually be better if gene flow can be controlled. This is logical. If the integrated program is essentially creating a local Chambers Creek or Skamania stock, an isolated program may be less harmful because gene flow will be better controlled. Third, the relative advantage of integrated over isolated programs depends on the gene flow rate achieved in the isolated program. The ability to conserve fitness relative to the integrated programs drops off rapidly as gene flow increases beyond a few percent.

The overall conclusion from this work is that if gene flow rates can be held to very low rates, isolated programs should be approximately equivalent or slightly better at conserving fitness loss due to domestication than integrated programs, but only if the gene flow can actually be constrained to those low rates (i.e., in Fig. 3-10, the isolated/integrated fitness index is greater than or equal to 1.0 at a 2% rate of gene flow in panels B, C, and D). Otherwise, integrated programs are superior for maintaining the fitness of the natural population.

In considering these results, three caveats need to be considered. First, the model deals only with domestication, not with the other genetic threat an isolated program may impose, outbreeding depression/loss of diversity due to the geographical source of the hatchery population. Second, the modeling deals only with relative, not absolute fitness. Our modeling tools and empirical data are simply too limited to make solid inferences at this point about actual fitness loss. Finally, this is a preliminary analysis.

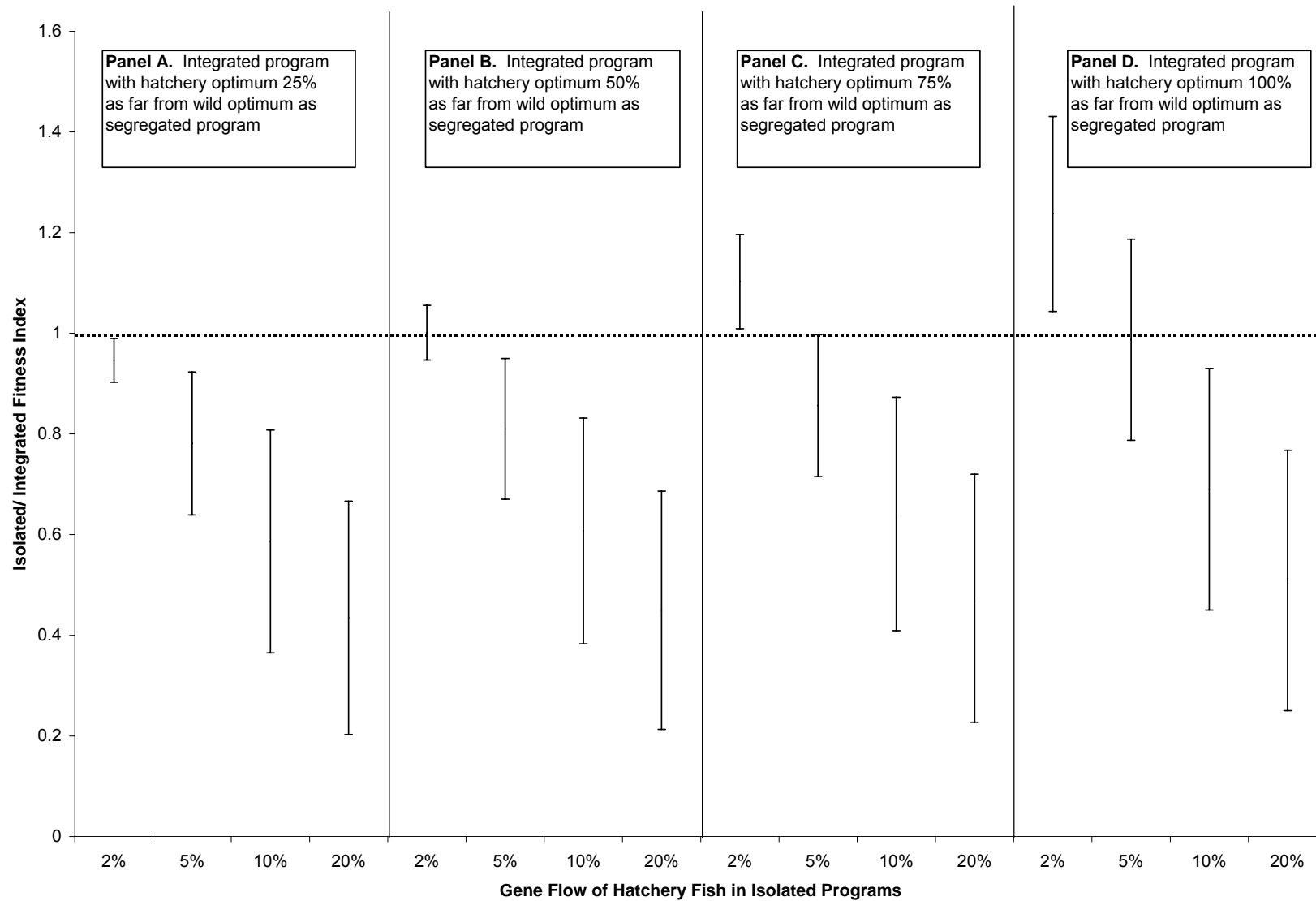


Figure 3-10. Comparison of the relative performance of isolated and integrated programs. Index values of <1.0 indicate that an integrated program operating under those conditions will preserve more of the fitness of a natural program than an isolated program.

The results seem clear and logical enough that we are reasonably confident that the general conclusions will hold over any parameter space we would explore, but we cannot be certain of this until we do additional modeling and until this work is more broadly reviewed.

3.3.5 Empirical Studies of Changes in Genetic Characteristics

In theory, the effects of hatchery steelhead on the genetic characteristics of naturally spawning populations of steelhead could be easily addressed. Samples could be taken from the population before and after the release of hatchery-origin fish to see whether or not the 'after release' populations of naturally spawning fish had become more similar to the hatchery population than the 'before release' populations. However, there are several complicating factors that make rigorous comparisons difficult or impossible. Samples of naturally spawning populations must exist so that initial genetic effects can be investigated. Enough loci must be screened to provide reasonable sensitivity to detect genetic change. Sample sizes must be large enough to provide adequate power to detect differences, if they occur. Genetic changes attributable to genetic drift or other factors must be distinguishable from those resulting from hatchery releases. Finally, a failure to detect change at the gene loci screened does not mean that changes have not occurred at other loci.

Which genetic characteristics should be evaluated? Many people would argue that genes encoding selectively important traits (e.g., life history variation, growth characteristics, reproductive performance) are the most important to monitor. However, many of these phenotypic characteristics have both environmental and polygenic components and are difficult and expensive to study. As a result, such data do not presently exist for addressing the question.

Another approach is to monitor enzyme-coding genes (investigate allozyme variation by electrophoretic analysis) and/or individual DNA segments that may or may not even have a coding function (e.g., mtDNA control region, microsatellite DNAs). This approach presumably provides a sensitive measure of gene flow (effective interbreeding) because the traits being monitored are selectively neutral (or nearly so). However, by definition, this approach does not directly evaluate possible changes in genetic traits that affect survival or performance.

Phelps et al. (1997) attempted to address the question by comparing steelhead allozyme data for the Chambers Creek Hatchery strain and various naturally spawning populations collected by Allendorf in the early 1970s (Allendorf 1975) with data collected by the WDFW Genetics Laboratory more recently (1993-1996). They reasoned that, if there had been substantial interbreeding and genetic introgression of the

Chambers Creek Hatchery strain into local, naturally spawning populations, the genetic distances between the hatchery strain and the various naturally spawning populations should have decreased over time. Genetic distance data (between the Chambers Creek Hatchery strain and the naturally producing local stock) for the seven rivers with data from the early 1970s and the early 1990s (from Table 4-1 of Phelps et al. 1997) are plotted in Fig. 3-11. This plot does not reveal a consistent pattern between the 1970s data and the 1990 data. In some cases, the collections from the 1970s have larger genetic distances (from the Chambers Creek Hatchery strain) than do the collections from the 1990s (e.g., Stillaguamish, Hoko, Twin, and especially Pysht) but in others the reverse is true (Sol Duc, Sauk, and SF Nooksack). Furthermore, in nearly all cases, the distances for the 1970s collections and those for the 1990s collections are of similar magnitude.

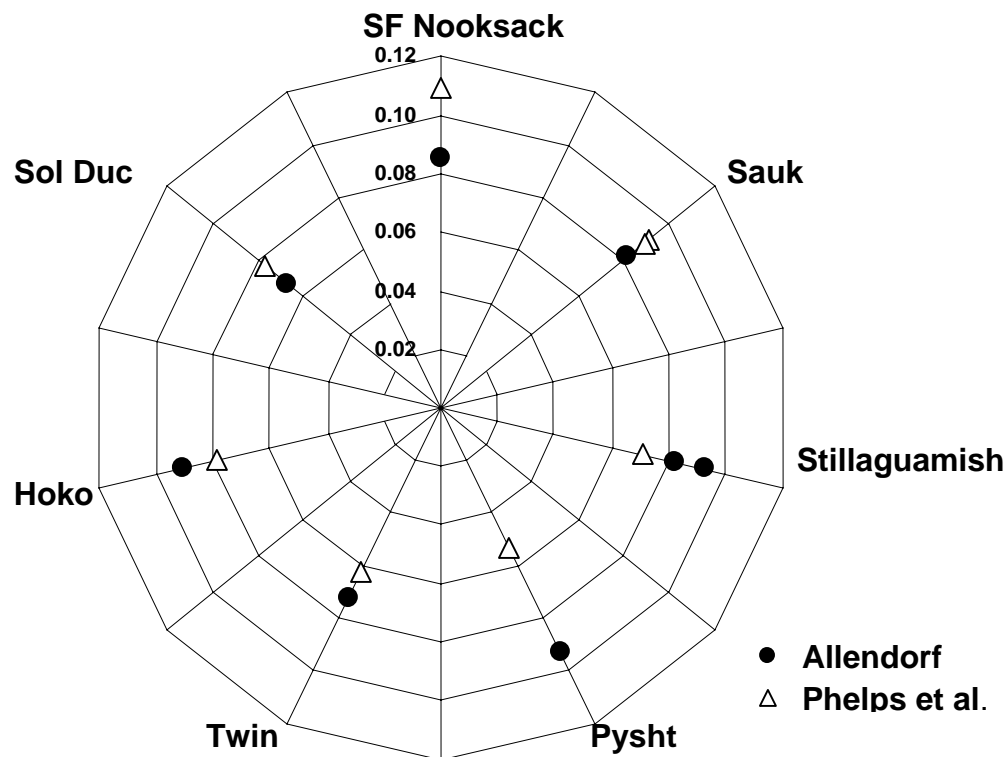


Figure 3-11. Cavalli-Sforza and Edwards (1967) chord distances using seven loci between the Chambers Creek Hatchery strain and selected naturally spawning steelhead populations in Washington. In this graph, the distance from the center of the graph to the data point represents the genetic distance between the Chambers Creek Hatchery strain and the listed stock. The seven loci in common between the two data sets are : *ADH*; *G3PDH-1*; *sIDHP-2*; *LDH-B2*; *sMDH-B1,2*; *PGM-2*; and *sSOD-1*. Where necessary, alleles in the Phelps et al. (1997) data set were pooled to ensure compatibility of the data with the data from Allendorf (1975).

Currens (pers. comm.) also evaluated changes in the genetic characteristics of the Pysht River Winter and Hoko River Winter steelhead populations from the data presented in Phelps et al. (1997). Currens computed the probability that changes in the genetic distance were simply due to genetic drift. The probabilities were based on simulated genetic drift from baseline allele frequencies at genetically effective population sizes, N_e , of 50 and 500. Comparing samples from 1975 and 1994, Currens concluded that the magnitude of the change was “extremely unlikely” to have resulted only from genetic drift alone (Table 3-4). “Although we cannot predict the direction of change due to genetic drift in any samples, the magnitude of the change, and the stronger similarity of Chambers Creek steelhead to Strait of Juan de Fuca samples than southern Puget Sound samples, it is highly likely that changes in these populations is due to interbreeding with Chambers Creek steelhead.”

Table 3-4. Changes in Pysht and Hoko River populations due to interbreeding with Chambers Creek steelhead. Table from Currens (pers. comm.)

Population	Genetic Distance to Chambers Creek Stock		Probability Due to Gene Drift		Estimated Gene Flow
	Early 1970s	Current	$N_e = 50$	$N_e = 500$	
Pysht River	0.03387	0.00534	< 5%	< 5%	11-27%
Hoko River	0.04382	0.00996	< 5%	< 5%	6-21%

What are the limitations of these analyses? First, the Chambers Creek Hatchery strain was established in 1945 (Crawford 1979) and WDFW records indicate that hatchery fish were planted into some streams as early as 1948 (Puyallup River). Between 1950 and 1973, over 15,500,000 hatchery winter steelhead smolts were planted into western Washington streams (WDFW unpublished steelhead stocking records). The numbers of hatchery winter steelhead smolts planted into the seven streams in the analysis are shown in Table 3-5, and range from just under 4,000 in East and West Twin rivers to over 1,000,000 in the Stillaguamish River. These data strongly suggest that the collections made in the early 1970s did not necessarily represent samples taken prior to possible hatchery effects. Thus, if there had been genetic effects during the first 5-25 years, they could have already been represented in the 1970s data used in the analysis. Furthermore, the test had limited power because only seven loci were common to the 1970s and the 1990s data sets, the collections from each location were generally small ($N = 35 - 56$; see Table 3-5), and the genetic characteristics of the Chambers Creek Hatchery strain (for the seven loci screened) had changed enough between 1975 and

1993 that the two collections were significantly different at $p < 0.01$ (Phelps et al. 1997).

Clearly, it would be desirable to extend this temporal analysis to earlier collections (prior to the early 1970s) to try to determine the 'before' hatchery genetic characteristics of naturally spawning populations. While no tissue samples suitable for allozyme analysis from earlier time periods are likely to exist, an attempt was made to locate archived scale samples that might allow DNA-based genetic analyses. Unfortunately, no such samples were found after talking with relevant WDFW staff. At this time it seems unlikely that a direct test of the issue involving 'before' as well as 'after' collections is possible.

Although the Phelps analysis shows that evidence of continued introgression from Chambers Creek stock is apparent (and we should pay attention to that) in some populations, it is also not as widespread or pronounced as one might expect, considering the numbers and distribution of hatchery stocking and resulting adult escapements of Chambers Creek stock that have gone on for the two decades between these two sampling events. This could occur either because our ability to assess the effects is poor, or that that native populations may have some level of resistance to introgression from the hatchery stocks (see Utter 2000 for a review of the factors that appear to affect the relative vulnerability or resistance to introgression).

Table 3-5. Details of the collections used for the 1970s vs. 1990s comparison and approximate numbers of hatchery smolts released into these streams between 1950 and 1973. Information on the 1970s samples is not available.

Stream	1990s collections			# Hatchery Smolts
	Year	N	Collection Code	
Chambers Creek Hatchery	1993	50	93CD	Na
SF Nooksack River	1995	35	95CL	67,500
Sauk River	1994	55	94AT	210,400
Stillaguamish River	1993	56	93CI	1,194,171
East & West Twin River	1995	56	95CF	3,700
Pysht River	1994	50	94CT	213,000
Hoko River	1994	53	94BB	66,464
Sol Duc River	1994	52	94CO	156,780

3.4 Competition

Intraspecific competition occurs indirectly when two or more individuals from the same species use the same resources when those resources are in short supply (exploitative competition), or directly when access to a critical resource is prevented (interference competition) (Pianka 1988). The resources that hatchery and wild steelhead may compete for include space, food, and access to mates. Competition may occur in freshwater rearing areas, the migration corridor, estuary, ocean, and spawning grounds. Interference and contest competition might be most prevalent in freshwater where territorial behavior is advantageous. Exploitative and scramble competition may be most prevalent in marine environments. Combinations of all types of competition may be expressed in the migration corridor and estuary, where temporary interference and exploitative competition may occur.

In hatchery programs that release smolts, competition with wild steelhead can occur when hatchery steelhead actively migrate as smolts, when they residualize, and when hatchery steelhead return to freshwater as adults. An actively migrating smolt is defined as a fish that emigrates to the ocean prior to a specified time (i.e., usually determined by the completion of the co-occurring wild steelhead smolt emigration). A residual is a juvenile steelhead that fails to emigrate within a specified time (Viola and Schuck 1995). In fact, residuals may never migrate to the ocean and instead become stream residents (Peven et al. 1994). In some instances, wild progeny of steelhead may become residuals, however the percentage of juvenile wild steelhead that residualize is unknown. For example, some adult resident rainbow trout in the Babine River, British Columbia, have been found to be offspring of maternal steelhead (Zimmerman and Reeves 2000).

Hatchery managers have traditionally attempted to efficiently produce smolts that actively emigrate to sea and later return as adults to provide harvest opportunities. However, residuals create inefficiencies and are an undesirable byproduct of many hatchery steelhead programs (Tipping et al. 1995; Viola and Schuck 1995; Busby et al. 1996). Residuals can form a significant percentage of hatchery steelhead releases, with estimates ranging between 3 and 52% (Seelbach 1987; Evenson and Ewing 1992; Martin et al. 1993; Tipping et al. 1995; Viola and Schuck 1995). Most steelhead hatcheries release smolts in the spring at age 1, despite the propensity for most wild steelhead smolts to emigrate at age 2 or older (Withler 1966; Peven et al. 1994; Busby et al. 1996). The impetus to migrate may be a combination of genetic and physiological factors (Peven et al. 1994; Pearsons et al. in press). The life histories of some wild steelhead may lead them to not emigrate at all and these fish are referred to as rainbow trout. Residualized steelhead are considered to present such a substantial risk to wild fish in some areas (e.g., in areas with populations listed under the ESA) that innovative

strategies have been developed to minimize the numbers of residuals that are introduced into streams (Viola and Schuck 1995; McMichael et al. 1999).

During freshwater rearing, salmonids in hatcheries and rivers use different methods to acquire food. River environments are heterogeneous (e.g., patchy) with respect to food and habitat quality. Salmonids rearing in streams primarily feed on drifting invertebrates as they maintain energetically profitable stream locations (Fausch 1984). Dominant fish secure the most food and grow the fastest (Metcalf 1986). These fish use a variety of agonistic interactions, such as nips, butts, chases, and threats to defend territories that have predictably high levels of food (Chapman 1962; Grant and Kramer 1990; McMichael et al. 1999). This type of interference interaction is referred to as contest competition. In contrast, salmonids in hatchery raceways live in homogenous environments where positions are equally viable. Fish in hatcheries frequently use shoaling or schooling behaviors and acquire food from the water surface. Thus, agonistic interactions prior to food interactions is wasted energy but with little immediate consequences in hatchery environments where food is plentiful. Fish that are in the right place at the right time and that swim rapidly towards the food are the most successful. This type of interaction is referred to as scramble competition.

The more similar the ecology of two organisms, the stronger the potential for competition. When individuals are of the same species, competition is likely to be most intense when they are of the same size. Competition is also hypothesized to increase as densities of fish increase, particularly as carrying capacity is reached. The carrying capacity of a watershed is one of the main factors in determining whether supplementation is a viable technique of increasing natural production. For example, supplementing a stock that is near carrying capacity will not produce a large increase in naturally produced fish. Carrying capacity in aquatic systems is defined as the maximum number of fish at their most demanding life-stage that can be supported by the available habitat.

Studying an indirect interaction such as competition is challenging and yet extremely important because of the impact that competition can have in structuring communities (Connell 1983; Schoener 1983). Controlled field experiments are the best way to test competition, but logistically impractical when considering multiple species in a variety of ecological conditions during many years. Historically, resource overlap has been used as an indication or demonstration of competition (Colwell and Futuyma 1971). The use of resource overlap indices during the 1970's led many scientists to conclude that competition was extremely prevalent in natural communities. However, without additional information, such as resource availability or behavioral interactions, overlap indices can be ambiguous (Colwell and Futuyma 1971; Sale 1974; Ross 1986). For example, high resource overlap between sympatric species is a good indication of competition only if resources are relatively scarce and important to the well being of

the organisms. Conversely, low resource overlap is a good indication that significant competition is not occurring only when it can be demonstrated that the lack of overlap is due to innate differences in preferences and not interactive segregation.

There are relatively few studies that have explicitly tested whether hatchery steelhead competitively impact the growth or abundance of wild steelhead (Weber and Fausch 2003), however mechanisms of competition have been demonstrated. Residualized hatchery steelhead have been observed to impact the growth of wild *O. mykiss* in stream enclosures (McMichael et al. 1997). However, in a larger scale experiment, impacts to growth or abundance were more equivocal (McMichael et al. 2000; Pearsons, pers. communication). Bjornn (1978) reported that stocking hatchery steelhead fry reduced the abundance of resident rainbow trout through competition. "Differences in behavior, physiology, and morphology that potentially affect competitive ability have been studied more than direct tests of competition" (Weber and Fausch 2003). McMichael et al. (1999) found that hatchery steelhead smolts interacted agonistically with *O. mykiss*, which caused wild *O. mykiss* to be displaced from presumably preferred locations.

Hatchery fish generally dominate wild fish in behavioral contests (Rhodes and Quinn 1998; McMichael et al. 1999). Dominance among salmonids has been demonstrated to be most consistently associated with fish size (Abbott et al. 1985; Berejikian et al. 1996; McMichael et al. 1999), but prior residence, prior winning experience, genetics, aggressiveness, and hatchery rearing also influence dominance (Huntingford et al. 1990; Berejikian et al. 1996; Rhodes and Quinn 1998). Differences in aggression are related to metabolic rate (Metcalf et al. 1995), genetics (Taylor and Larkin 1986; Rosenau and McPhail 1987), and rearing experience (Berejikian et al. 1996; Rhodes and Quinn 1998).

Domestication selection has been shown to alter the aggressiveness and dominance of hatchery fish. Domestication has been implicated as increasing and decreasing aggressive and schooling behavior in fish (Ruzzante 1994). Berejikian et al. (1996) found that offspring of wild steelhead trout were more aggressive and dominant (87.5%) than size matched offspring of parents that had been in hatchery culture for 4 to 7 generations. However, when hatchery fry had a 3.0-4.5% size advantage, they dominated wild fish in 68% of encounters. Swain and Riddell (1990) found that domesticated coho were more aggressive than those of natural origin from nearby streams. Hatchery reared chinook salmon dominated smaller wild chinook salmon and altered wild fish behavior (Peery and Bjornn 1996). Farrell (2003) found that wild spring chinook salmon from the Yakima Basin were competitively dominant to descendents of first generation local origin hatchery fish in contest competition trials.

Despite the limited reproductive success of some domesticated hatchery-origin spawners, the sheer number of hatchery-origin spawners can result in substantial

numbers of juvenile progeny. This scenario creates a mechanism for detrimental competitive effects of the offspring of hatchery fish on rearing juvenile wild fish (Leider et al. 1990; Kostow et al. 2003; McLean et al. 2004). This could be expected to cause some level of depression of productivity in the wild population as long as the competition continues. Each of the domesticated hatchery stocks reported on here have earlier spawn timing than the local wild stocks. Thus any of the hatchery offspring that do survive to emerge will do so much earlier than most wild fish and would be expected to have both a size-related and prior residence-related competitive advantage that may reduce the cumulative effects of other mal-adaptive traits that confer their lower observed fitnesses.

In conclusion, there is sufficient theoretical and empirical data to indicate that hatchery steelhead could potentially pose a competitive risk to wild steelhead. However, risks could range from low to high, and our ability to accurately assess these risks is still lacking empirical data.

3.5 Predation

Both hatchery steelhead juveniles and adults have the potential to prey on juvenile salmonids. Although research on the subject has been somewhat limited, predation on stocks of low abundance is of most concern and thus, predation on juvenile Chinook salmon has been the focus of most investigations.

Based on the only two studies found on the subject, adult steelhead consumption of juvenile salmonids in freshwater is infrequent; Burns (1974) reported that 95% of adult steelhead contained food items in two tributaries of the Sacramento River in California but that no juvenile fish were found. Vander Haegen et al. (1998) examined the stomach contents of adult summer steelhead on the Cowlitz River. Of 1,041 stomachs examined, 11% contained food items but only two stomachs (0.2%) contained the remains of four juvenile salmonids.

Juvenile hatchery steelhead (smolts) are relatively large (170-230 mm) and usually released with spatial and temporal overlap to allow predation on Chinook salmon fry. However, most evidence suggests minimal predation on juvenile Chinook salmon. Even though Martin et al. (1993) found that hatchery steelhead had consumed Chinook salmon juveniles up to 108 mm in fork length and averaged 35% of their body length, Martin et al. (1993), Cannamela (1993) and Jonasson et al. (1995) found low rates of predation, with 0.00% to 0.18% of hatchery steelhead smolts containing juvenile Chinook salmon. On the Green River for 2003 and 2004 combined, 1,134 hatchery steelhead stomachs were examined (Topping, pers. communication). Most (78.8%) hatchery steelhead smolts contained insects, 20.5% of stomachs were empty and 3 (0.3%)

contained chum salmon fry. In 2003, an additional five fish contained salmonid fry but all prey were either alive or freshly killed and thought to have been consumed in the trap, so they were not counted. All prey fish were identified as chum salmon fry with no Chinook salmon juveniles present. Mean length of hatchery steelhead smolts having consumed fry was 191 mm (range 176-205 mm). On the Deschutes River, Washington, 1,407 hatchery steelhead smolts were captured in a fish trap and 91 fish were captured by angling, a total of 1,498 fish. Gastric lavage sampling indicated that 69% of hatchery steelhead smolts contained insects and 31% were empty; no salmonid fry were found (Sharpe, pers. communication).

Further, an ongoing study (Kraemer, Tipping, and Busack, in preparation) found that egg-to-migrant survival of Chinook salmon juveniles remained unchanged in the Skagit River even when hatchery steelhead smolt numbers trebled from 196,000 to 583,000 fish.

An outlier to the above research is the study on the Lewis River by Hawkins and Tipping (1999) who reported that 232 hatchery steelhead stomachs contained 58 Chinook salmon juveniles, an average of 0.25 fry/steelhead. However, the high predation rates on the Lewis River are probably due to the great abundance of Chinook fry and the late spawning time of the adult fish. In the Martin et al. (1993) study on the Tucannon River, spawning escapement was estimated at 259 Chinook salmon in 1991 (WDFW records), representing an egg density of 7,600 eggs/km, based on a spawning access of 84 km, an assumed 45% of the population being female and a fecundity of 5,500 eggs/female. On the Lewis River, Chinook salmon spawner abundance typically averages about 11,000 fish, resulting in about 27,225,000 eggs for 31 km of accessible river, 878,200 eggs/km, 115 times greater than that on the Tucannon River.

In addition, Chinook salmon in the Lewis River spawn in November whereas most Chinook salmon in Washington spawn in late September and early October. The late spawning time is probably due to the river temperature profiles resulting from the dams on the river. Thus, peak juvenile emigration occurs in late June and early July on the Lewis River (McIsaac 1990), 4 to 6 weeks later than most other streams. Most Chinook salmon juveniles were probably present on the Lewis River when hatchery steelhead were released from mid-April to early May whereas many had emigrated by that time on other rivers. Therefore, not only was there a much higher density of Chinook salmon juveniles present in the Lewis River than on other streams when hatchery steelhead were released, but the Chinook salmon juveniles were smaller in size, probably making them more susceptible to predation.

Obviously, the predation opportunity of hatchery steelhead is influenced by their spatial and temporal overlap with wild salmonid juveniles. Migration travel rates of hatchery steelhead have been documented at around 20 miles per day (Dawley et al. 1984; Harza

1998). However, substantial smolt losses have been frequently documented before fish exit the river. A 20% loss was observed in 4.7 km of travel on Snow Creek (Tipping et al. 1995), 40-50% loss in a series of releases with 9.9-17.2 km of travel on two coastal streams (Tipping and Byrne 1996), 42.0-42.7% loss over 10 km of travel on a stream in British Columbia (Ward and Slaney 1990), and 36% loss over 11 km of travel in the Yakima River (McMichael et al. 1992).

Factors that affect emigration rates of hatchery steelhead smolts include length and condition factor at release (Tipping et al. 1995). Smolts less than 190 mm and fish with a condition factor greater than 1.0 had substantially lower emigration rates. Ongoing research on the Kalama River suggests that residualism rates are higher for hatchery fish spawned from wild brood stock. Many rearing parameters that affect residualism rates are probably inverse to those mentioned in section 3.2.2 that affect survival.

Commonly, 5-10% of a hatchery steelhead population fails to emigrate from rearing vessels after release. Voila and Shuck (1995), in a study on summer steelhead in eastern Washington, found that in one year, many non-migrants were precocious males and they recommended not releasing them so that the number of residuals would be reduced. However, in a recent study on the Washington coast, adult returns of hatchery steelhead that were forced from a raceway (7% of population) after volitional opportunity had similar survival as volitional emigrants.

Current methods employed by WDFW to reduce predation risk by hatchery steelhead smolts on juvenile salmonids include delayed release timing and downstream transport. At the Dungeness Hatchery, hatchery steelhead smolts are not released until June 1 in years following pink salmon spawning so that pink salmon fry can clear the system before steelhead are present. At Merwin Hatchery on the Lewis River, hatchery steelhead smolts are trucked for release below the juvenile Chinook salmon rearing area.

3.6 Facility Effects and Disease

Hatchery facilities have potential to impair wild fish. Upstream and downstream passage barriers may exist, intake screens may impinge juveniles or allow their passage into the hatchery, effluent water quality may be degraded, wild fish adults may enter adult ponds and be inadvertently destroyed during handling of hatchery fish, and diseases may be amplified.

Current hatchery facility passage and screening criteria include NOAA Fisheries' Anadromous Salmonid Passage Facility Guidelines and Criteria, WDFW's Fish Protection

Screen Guidelines for Washington State and Fishway Guidelines for Washington State. In fall 2004, water intakes in Puget Sound and Coastal anadromous hatcheries were assessed for screening and passage by WDFW engineers and a consultant. Nearly every hatchery needed some corrective action to be compliant with the guidelines; estimated costs were about \$22 million.

However, hatchery barriers on streams have aided management of adult wild fish by allowing wild fish to be counted and hatchery fish numbers passed upstream to be controlled. Such barriers exist at Kalama Falls Hatchery on the Kalama River, the Cowlitz Salmon Hatchery on the Cowlitz River and at Minter Creek Hatchery.

Effluent from hatcheries has the potential to degrade water quality for wild fish and the habitat in which wild fish rear. Poor water quality with high biotic loads or chemicals from treatments could slow growth of wild fish or increase their susceptibility to disease while the discharge of sediments could result in stream siltation, reducing fish rearing habitat. The Clean Water Act set water quality standards for all contaminants in surface waters. The Act made it unlawful for any person to discharge any pollutant from a point source into navigable waters, unless a permit was obtained under its provisions. Environmental monitoring is conducted at WDFW hatcheries to ensure the facilities meet requirements of the National Pollution Discharge Elimination Permit administered by the Washington Department of Ecology. Monitoring parameters include total suspended solids, settleable solids, in-hatchery water temperatures, and in-hatchery dissolved oxygen. To comply with the Clean Water Act and the National Pollution Discharge Elimination Permit, recent and ongoing assessments of WDFW Puget Sound and Coastal facilities have identified needed corrective actions. Construction or upgraded of pollution abatement facilities at WDFW facilities will cost \$5 to 10 million; corrective actions are currently underway at some facilities and planned for the rest.

When handling large numbers of hatchery brood stock, hatchery staff may inadvertently kill wild fish that are in the pond due to repeated handling or other means. Such destruction of wild fish can be minimized with improved hatchery design during renovations and acquisition of fish friendly equipment. For example, wild fish can often be excluded from the hatchery brood stock with a sorting tower and flume like those found at Minter and Cowlitz Salmon hatcheries.

There is potential that disease organisms can be amplified in hatcheries and then discharged to infect wild fish. Although this has received limited study and there have been no documented cases in Washington, hatchery personnel work closely with Fish Health staff to minimize the incidence of disease within hatcheries, and thus, the discharge of disease should also be minimized. Reporting and control of fish pathogens are conducted in accordance with the co-managers Fish Disease Control Policy and include protocols on fish and egg movements, therapeutic and prophylactic treatments,

and sanitation. Hatchery protocol calls for mortalities to be removed from the water and disposed of properly.

3.7 Discussion

Hatchery-based production is a tool that can be used to increase fishing opportunities, conserve at-risk natural populations, or facilitate research, monitoring, and evaluation. Use of the tool is not without risks. Possible impacts can include reductions in the diversity and fitness of natural populations, deleterious ecological interactions with natural populations and other species, and migration impediments resulting from the construction of hatchery facilities.

Hatchery reform is the ongoing, systematic application of scientific principles to improve hatcheries for recovering and conserving naturally spawning populations and supporting sustainable fisheries (HSRG 2004). The roots of hatchery reform can be traced back at least to the late-1980s, but an influential report published by the National Academy of Sciences in 1996 may have been the first to promote a broad discussion of a new paradigm for hatchery programs. That report, *“Upstream: Salmon and Society in the Pacific Northwest”* (National Research Council 1996), concluded that hatcheries had generally failed to compensate for habitat degradation and recommended a broader, ecosystem perspective for hatchery management:

“Hatcheries can be useful as part of an integrated comprehensive approach to restoring sustainable runs of salmon, but by themselves they are not an effective technological solution to the salmon problem.”

The concept of hatchery reform has subsequently been refined (Brannon et al. 1999; ISG 2000; Williams et al. 2003; HSRG 2004) and, in this chapter, new tools have been developed to evaluate artificial production programs for steelhead.

Drawing on these efforts, we discuss below seven considerations to effectively use artificial production programs as a tool to achieve conservation and fishery objectives.

1) Healthy Habitat Provides Greatest Biological Certainty. *Productive natural habitat is essential for healthy, harvestable salmon populations. However, restoring and protecting habitat to the extent necessary to achieve population restoration and harvest goals is often a long-term process and social, economic, or funding constraints may make it infeasible for some populations.*

Four alternative types of habitat management strategies are to protect, restore, rehabilitate, or substitute (NRC 1992). As the strategy moves from protection to substitution (including hatchery production), the certainty of achieving viable salmonid populations declines because of the complex interaction between the environment and salmonid populations and our limited ability to predict the effects of anthropogenic intervention (NRC 1992; 1996). Although protection and restoration strategies provide the greatest biological certainty, habitat within the range of listed species of salmonids is typically substantially degraded and the restoration of natural processes may not be feasible within a 10-20 year time frame. In some watersheds, social, economic, and funding constraints may limit our ability to provide the habitat conditions necessary to meet fishery and conservation objectives (see for example, NMFS' consideration of economic impacts in the proposed rule for critical habitat, 69 FR 74572; December 14, 2004).

2) Ecosystem Perspective Promotes Improved Performance. *Hatcheries designed, operated, and evaluated in an ecosystem perspective are more likely to provide harvest and conservation benefits with reduced risks to natural populations.*

A fundamental change from the historical paradigm for hatchery programs is required to achieve conservation and fishery objectives. Rather than viewing a hatchery as an isolated fish production factory, numerous scientific reviews have recommended that hatchery programs should be evaluated as part of the environmental and ecological systems in which they operate (NRC 1996; Brannon et al. 1999; HSRG 2004). Viewing a hatchery as a tributary to a watershed expands hatchery assessments from a simple examination of fish culture practices to a broad investigation of demographic, ecological, evolutionary, and fishery interactions (Williams et al. 2003).

3) Successful Programs Achieve Watershed Specific Objectives. *A hatchery program is "successful" when it provides more benefits than risks when evaluated relative to watershed-specific objectives. The characteristics of a successful program will differ among watersheds because of the varying status of natural populations and policy decisions regarding the rapidity and extent of habitat protection and recovery.*

Hatchery programs can provide substantial economic, cultural, and conservation benefits, but potentially they can also pose risks to natural populations of salmon and steelhead. Often, hatchery programs focused on preventing extinction and promoting recovery must consider tradeoffs between different biological risks in the short-term to achieve long-term recovery. The risks and benefits of a hatchery program should be evaluated relative to the ability of the habitat to support viable natural populations and meet other policy objectives - currently and in the future. This evaluation should take into account the abundance, productivity, diversity, and spatial structure of the population, and how the hatchery program affects these population characteristics.

As habitat improves to levels that support viable natural populations, hatchery programs can often be modified to reduce potential risks while maintaining harvest and conservation benefits. A hatchery program may be visualized as following a trajectory from the current operation to the expected operation at recovery (Fig. 3-12). The speed and direction of the trajectory will depend on the current conservation value of the population, the current productivity of the habitat, and policy decisions that define region-wide recovery.

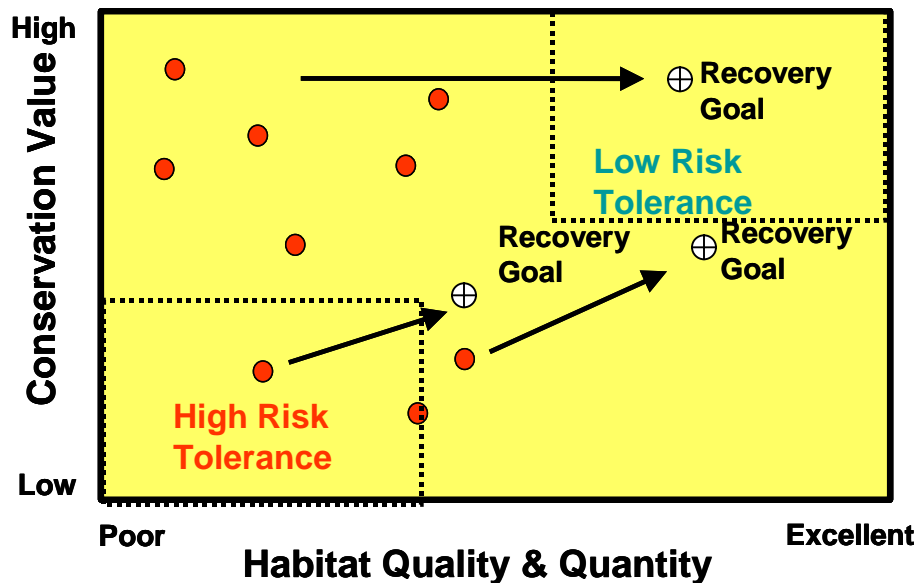


Figure 3-12. Conceptual representation of relationship between habitat quality and quantity, population conservation value, and risk tolerance for hatchery programs (revised from Currrens and Busack, In Prep.).

4) Goal and Strategy Drive Program Protocols. *The design of a successful program begins with the careful selection of either an integrated or an isolated hatchery strategy. Integrated hatchery programs can be operated to increase the number and distribution of natural spawners, increase the productivity of the composite population, and provide fishing opportunities. Isolated hatchery programs can be operated to provide fishing opportunities while minimizing interactions with natural populations.*

Strategy selection is program and watershed specific, and depends on the status of the natural population and habitat, the ability to collect natural-origin broodstock, the ability to control the number of hatchery-origin adults in natural spawning areas, and

other factors. Hatchery operating protocols should be consistent with the management objective and the strategy. The protocols describe the daily operation of the hatchery program, and include the program size, broodstock source and collection procedures, rearing conditions, and time, size, and location of release.

5) Productive Habitat is Essential. *Habitat quality and quantity remain essential, regardless of the hatchery strategy, if hatchery programs are to be successfully implemented. In watersheds where social, economic, or funding constraints limit the feasibility of meeting conservation and harvest objectives strictly through habitat restoration and protection, hatchery programs using an integrated strategy and complementary habitat actions ("balanced portfolio" approach) could be implemented and tested.*

An outgrowth of the new, ecosystem paradigm for hatchery operations is the renewed recognition of the critical importance of habitat. Hatchery programs can only be successful if habitat conditions are conducive to the survival of salmon throughout their entire life cycle. This is particularly true for programs relying on an integrated strategy, since natural-origin broodstock must be incorporated into the hatchery in each generation. This means that the risks and benefits of a program of fixed size will be directly related to the productive capacity of the natural habitat.

In watersheds where social, economic, or funding constraints limit the feasibility of meeting conservation and harvest objectives strictly through habitat restoration and protection, hatchery programs using an integrated strategy and complementary habitat actions could be implemented and tested. Where applied, this "balanced portfolio" approach should be carefully designed, monitored, and evaluated during the next 10-20 years. Scientific decision support tools developed by the comanagers, HSRG, and other can help identify scientifically defensible combinations of habitat improvement, harvest constraints, and hatchery program size that are consistent with policy objectives and constraints.

6) Relationship Among Hatcheries, Harvest, and Habitat. *The effectiveness of hatchery programs is likely to increase if they are developed and evaluated as part of an integrated harvest, hatchery, and habitat strategy for conservation and sustainable fishing opportunities.*

The complex interaction of harvest, hatchery, and habitat is discussed further in Chapter 4, Management.

7) Manage Hatchery Programs for Success. *Hatchery management improves through adaptive management - or making changes based on learning by doing. Adaptive management is enhanced by carefully defining and monitoring performance measures.*

Continued review, evaluation, and modification of hatchery programs is essential to assure that fishing-related economic and cultural benefits are maximized and region-wide conservation objectives achieved. Adaptive management is a process that allows managers to make informed decisions while operating in the face of uncertainty, including future circumstances and consequences. It is likely to be most effective if it is driven by clearly defined goals and objectives, performance measures are identified and monitored, and results are readily available, communicated, and evaluated in a defined decision making framework.

The HSRG (2006) provided broad recommendations for steelhead programs in Puget Sound and the Washington Coast. The recommendations were premised on the assumption that integrated harvest programs are not currently a viable alternative in most watersheds in Puget Sound because the natural steelhead populations are not sufficiently abundant and productive to provide the necessary number of natural-origin broodstock. Key points of these recommendations are summarized below.

Wild Steelhead Management Zones (WSMZs). The HSRG suggested selecting “a balance of large and small streams and habitat types in each region that are not planted with hatchery fish and are instead managed for native stock. Fishing for steelhead in these streams would not be incompatible with this approach, but no hatchery-produced steelhead should be introduced.”

Locally Adapted, Early Run Timing Broodstock. Outside of the WSMZs, the HSRG recommended using locally adapted broodstock and to reduce reliance on outside sources of broodstock to backfill shortages in the locally adapting hatchery stock. The hatchery stock should be managed to “maintain its early spawn timing and reduced the likelihood of interaction with naturally-spawning steelhead.”

Adult Collection Capability. To minimize reproductive interactions with natural-origin spawners, the HSRG recommended that an adult capture facility should be in place in every location where juveniles from an isolated program are released.

Program Size. The number of juveniles released from a hatchery program should be established “in a manner that achieves harvest goals with minimal impact on wild populations.”

Size of Juveniles at Release. “Release hatchery yearling steelhead smolts between April 15 and May 15 at target size of six fish to the pound, and a condition factor of less than 1.0.”

Monitoring and Evaluation. The HSRG recommended that monitoring and evaluation should be a “basic component” of the management of artificial production programs. In addition, a specific recommendation was to “investigate the reasons for the recent decline in adult winter steelhead returns, formulate a working hypothesis for the decline and take appropriate actions.”

The WDFW expects that the general recommendations of the HSRG will be used in conjunction with this report and others to develop improved artificial production strategies for steelhead. However, specific program modifications will need to be developed on a population specific basis, with consideration of conservation and fishery objectives, the biological characteristics of the natural population, the productivity of the habitat, and the potential for implementation of alternative harvest management strategies. Rather than a simple mixture of isolated, early-timed hatchery programs and WSMZs, a wider variety of artificial production programs will likely need to be considered. Kelt reconditioning, integrated conservation programs, integrated harvest programs, and isolated harvest programs are all strategies that, when thoughtfully implemented, may help achieve conservation and fishery objectives.

3.8 Findings and Recommendations

Finding 3-1. The recreational fishery for hatchery-origin steelhead provides substantial fishing opportunities and economic benefits. In the nine seasons from 1995-1996 through 2003-2004, recreational anglers harvested an average of 99,300 hatchery-origin steelhead. The estimated expenditures by recreational fishers associated with the catch of hatchery-origin steelhead were approximately \$99 million dollars per year, with an economic output (includes revenues generated indirectly) of \$188 million dollars per year.

Finding 3-2. Hatchery programs using Chambers Creek Winter or Skamania River Summer steelhead coupled with an isolated strategy comprise over 68% of the broodstock collection programs in western Washington. Over 68% (28 of 41) of the steelhead broodstock collection programs in Puget Sound, the Olympic Peninsula, Southwest Washington, and the Lower Columbia regions collect broodstock of either Chambers Winter or Skamania Summer origin. Juveniles from these programs are generally released in watersheds where these stocks are not indigenous. The programs are operated with an isolated (also called segregated) reproductive strategy with the intent that little or no gene flow will occur between the natural and hatchery population. In contrast, hatchery programs in eastern Washington primarily rely on an

integrated strategy with broodstock of local origin (5 of 7 or 71% of broodstock collection sites).

Finding 3-3. Naturally spawning adults originating from hatchery programs using the Chambers Creek Winter or Skamania River Summer stock have low reproductive success. Six empirical studies in Oregon and Washington demonstrated that returning adults from these programs have low reproductive success in natural spawning areas. In these studies, highly domesticated hatchery-origin spawners have been found to have only 7% to 37% of the success of natural-origin spawners in the same river.

Finding 3-4. Chambers Creek Winter and Skamania river Summer steelhead programs pose a high potential genetic risk. Although each returning adult of Chambers Winter and Skamania Summer origin may on average have low reproductive success, substantial production of juveniles can still result from the spawning of a large number of hatchery-origin adults. When considered together with the previous two findings, this suggests that the Chambers Winter and Skamania Summer steelhead hatchery programs could pose a substantial risk to both the among-population diversity and the fitness of natural steelhead populations. Direct empirical evidence for loss of diversity is limited because genetic samples were generally not collected from natural populations before hatchery programs were initiated and the power of tests that can be applied is limited by the small number of loci (7) evaluated. Despite these limitations, 2 of the 7 (29%) natural populations sampled had significant introgression by Chambers Winter type fish during the time period evaluated.

Finding 3-5. Integrated programs are likely to be more effective at maintaining population fitness for rates of gene flow >2%. Theoretical analysis calibrated with field studies indicates that integrated programs using a local source of broodstock will be more effective than isolated programs in maintaining the fitness of natural populations when the rate of gene flow from adults of hatchery-origin to the naturally-spawning population exceeds 2% per year.

Recommendation 3-1. Evaluate the potential range of gene flow from returning adults to natural populations in all watersheds where Chambers Winter or Skamania Summer type steelhead are released. Where risks are inconsistent with policy objectives for the natural population, implement one or more of the following actions: 1) release steelhead juveniles from isolated programs only at locations where returning adults can be captured; 2) adjust the size of the program, release location, fishery harvest rate, or other factor to achieve an acceptable rate of gene flow; or 3) replace the isolated program with an integrated program developed from local broodstock.

Recommendation 3-2. Design and initiate a program to monitor the genetic characteristics of steelhead populations. Prioritize the collection of samples from watersheds with both a hatchery program and a significant natural population to assess the potential loss of diversity associated with hatchery programs.

Recommendation 3-3. Support and expand research to link changes in genetic markers to the abundance and productivity of the population. Current genetic monitoring typically assesses changes in the frequency of neutral alleles, or alleles that are not believed to have a functional effect on fitness. If we could identify genetic markers that were related to fitness, we could provide an improved assessment of what changes in the frequency of these markers mean to population productivity and other characteristics.

Recommendation 3-4. Submit for publication in a peer-reviewed journal a paper describing the methods developed to compare the potential fitness loss associated with integrated and isolated artificial production programs. These methods may be of broad interest in the evaluation and management of artificial production programs.

Finding 3-6. Progeny from Chambers Creek Winter and Skamania River Summer adults that spawned naturally pose a potential risk of competition to the indigenous natural population. Despite the limited reproductive success of some domesticated hatchery-origin spawners, the sheer number of hatchery-origin spawners in natural spawning areas can result in substantial numbers of juvenile progeny. Competition may occur with indigenous natural populations, but the potential magnitude of the effects is extremely difficult to quantify.

Recommendation 3-5. Evaluate the potential effects of competition when considering the relative risks and benefits of isolated programs, particularly if conservation concerns exist. Where risks are inconsistent with policy objectives for the natural population, implement one or more of the actions described in Recommendation 3-1.

Finding 3-7. Integrated artificial production programs can increase the number of natural spawners and improve the productivity of the composite population, but the long-term effectiveness of these programs has not been conclusively demonstrated. Successful implementation of an integrated program requires careful consideration of the number and characteristics of natural-origin broodstock, the incidence of hatchery-origin adults in natural spawning areas, and the juvenile release strategy (location and time of release; size and smolting status of juveniles at release). While integrated programs have proven effective in increasing the abundance and productivity of the

composite population in the short-term, long-term impacts on diversity, spatial structure, and the potential loss of productivity associated with domestication have not been thoroughly evaluated. Long-term effectiveness also depends on maintenance and improvement of the productivity of natural habitat. Interactions between habitat, hatchery, and harvest are discussed further in Chapter 4.

Recommendation 3-6. Evaluate the potential effects of integrated programs on the diversity, spatial structure, abundance, and productivity of the indigenous natural population. Carefully consider the size of the program and characteristics of the release strategy (location, time, size of fish) to assure that potential genetic and ecological risks are consistent with policy objectives.

Finding 3-8. Survival rates for steelhead released from Puget Sound programs are currently the lowest of any region within the state. Survival rates for winter steelhead released from hatchery programs in Puget Sound dropped to an average of <0.4% for the 1995 through 1998 brood years. The survival rates are currently the lowest of any region within the state, including the Upper Columbia River and the Snake River, and appear to have resulted from a significant shift in the conditions encountered during early marine rearing in Puget Sound and the Georgia Basin.

Recommendation 3-7. Develop a “population rescue” reference document that discusses the conditions under which a hatchery conservation program may be warranted and the key questions that should be addressed during the development of the program. (Chapter 3, Recommendation 7)

Recommendation 3-8. Evaluate the fishery and economic benefits of isolated hatchery programs in Puget Sound relative to those of hatchery programs for other salmonid species and the potential benefits of conservation programs for natural steelhead populations. If necessary, adjust programs to provide enhanced economic and conservation benefits.

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Appendix 3-A. Derivation of Gene Flow Equation

The spatio-temporal distribution of spawners in a stream with an isolated hatchery program is shown in Fig. 3-7. Region A represents the distribution of natural-origin spawners, Region C the distribution of hatchery-origin spawners, and Region B represents the overlap of the two distributions.

Let N_N be the number of natural-origin spawners, N_H be the number of hatchery-origin spawners, o_N be the proportion of natural-origin spawners in region B, and o_H be the proportion of hatchery-origin spawners in region B. The number of spawners in the three regions is then:

$$A: N_N(1-o_N), B: N_N o_N + N_H o_H, C: N_H(1-o_H)$$

We assume that the proportion of total matings in each region are the same as the proportions of fish in each region. At this point we remove the absolute fish numbers and rescale as proportions, letting q be the proportion of total spawners that are hatchery-origin fish and $1-q$ be the proportion of total spawners that are natural-origin fish. Now the proportions of matings in each region are:

$$A: (1-q)(1-o_N), B: (1-q)o_N + qo_H, C: q(1-o_H)$$

Matings within region A are NxN only, matings within region C are HxH only, but matings within region B are NxN, HxN, NxH, and HxH. To calculate the proportions of the various mating types, it is necessary to calculate the proportions of natural-origin and hatchery-origin spawners within region B. Let these two proportions be p_N and p_H , respectively.

$$p_N = \frac{(1-q)o_N}{(1-q)o_N + qo_H}, \quad p_H = \frac{qo_H}{(1-q)o_N + qo_H}$$

To simplify algebra for the time being, let $X = (1-q)o_N + qo_H$

Assuming fish mate randomly and ignoring the distinction between NxH and HxN matings, total mating proportions are:

$$NN: (1-q)(1-o_N) + p_N^2 X$$

$$HN: 2p_N p_H X$$

$$HH: q(1 - o_H) + p_H^2 X$$

Substituting for p_N and p_H , these proportions become:

$$NN: (1 - q)(1 - o_N) + \frac{(1 - q)^2 o_N^2}{X}$$

$$HN: \frac{2q(1 - q)o_N o_H}{X}$$

$$HH: q(1 - o_H) + \frac{q^2 o_H^2}{X}$$

Gene flow equals the proportion of alleles in the population that are from immigrants. This is a function of the mating proportions, the success of each mating type, and the relative contribution of each mating type. Here we assume that immigrant alleles come only from HxN matings and HxH matings with Region B, and that the entire gene pool is produced by fish in Regions A and B. Each fish from a HxN mating brings half as many immigrant alleles into the population as an HxH mating. Let w be the relative fitness, and f be the relative frequency of a mating type. Gene flow can then be expressed as:

$$GeneFlow = \frac{f(HH)w(HH) + f(NH)w(NH)(0.5)}{f(HH)w(HH) + f(NH)w(NH)(0.5) + f(NN)w(NN)}$$

Now let $w(HH)$, $w(NH)$, and $w(NN)$ be k_1 , k_2 , and 1, respectively. Substituting from equations above for $f(HH)$, $f(NH)$, and $f(NN)$:

$$f(NN)w(NN) = (1 - q)(1 - o_N) + \frac{(1 - q)^2 o_N^2}{X}$$

$$f(NH)w(NH) = k_2 \left[\frac{q(1 - q)o_N o_H}{X} \right]$$

$$f(HH)w(HH) = k_1 \left[q(1 - o_H) + \frac{q^2 o_H^2}{X} \right]$$

Substituting these expressions into the gene flow equation yields:

$$GF = \frac{k_1 \left[q(1-o_H) + \frac{q^2 o_H^2}{X} \right] + k_2 \left[\frac{q(1-q)o_N o_H}{X} \right]}{k_1 \left[q(1-o_H) + \frac{q^2 o_H^2}{X} \right] + k_2 \left[\frac{q(1-q)o_N o_H}{X} \right] + \left[(1-q)(1-o_N) + \frac{(1-q)^2 o_N^2}{X} \right]}$$

Multiplying through by X/X to remove X terms from denominators, we get:

$$GF = \frac{k_1 [q(1-o_H)X + q^2 o_H^2] + k_2 [q(1-q)o_N o_H]}{k_1 [q(1-o_H)X + q^2 o_H^2] + k_2 [q(1-q)o_N o_H] + [(1-q)(1-o_N)X + (1-q)^2 o_N^2]}$$

Finally, substituting $o_N + q(o_H - o_N)$ for X , we arrive at the equations provided in the text:

$$a = o_N + q(o_H - o_N)$$

$$b = k_1(aq(1-o_H) + q^2 o_H^2) + k_2 q(1-q)o_N o_H$$

$$Gene\ flow = \frac{b}{b + a(1-q)(1-o_N) + (1-q)^2 o_N^2}$$